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Hydrological and ecological observations along the eastern Beaufort Sea coast of Alaska

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Hydrological and ecological observations along the eastern Beaufort Sea coast of Alaska

by

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Dedication

To my Mom for making school fun and my Dad for making science cool

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Abstract

Hydrological and ecological observations along the eastern Beaufort Sea coast of Alaska

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The US Beaufort Sea coast is fringed by barrier islands, which enclose numerous bays and lagoons that provide habitat for migratory fish and waterfowl that are essential to the subsistence and culture of Iñupiat communities of northern Alaska. In the eastern Beaufort, in particular, residents of Kaktovik rely heavily on the high benthic productivity of these lagoon systems to support the fish and bird populations that they depend on for subsistence. We monitored aspects of hydrology and ecology in several lagoons in the eastern Alaskan Beaufort Sea coast from 2011 to 2014. Our hydrographic data from continuous in situ measurements of temperature and salinity revealed that lagoons possess unique regimes that vary seasonally and reflect unique hydrologic and geomorphic characteristics. H_2O-$\delta^{18}O$ and salinity measurements revealed that meteoric water is the dominant source of low-salinity water in all lagoons in June and August, though sea ice melt water was also present. Most differences among lagoons were caused by variation in circulation and connection to adjacent marine waters. We also used stable C and N isotopic analysis to determine trophic structure and assess dependence of fauna

on terrestrial (C_T) vs. marine sources of carbon, with particular focus on animals widely used by local subsistence hunters. Our mixing model results suggest that terrestrial carbon (C_T) may be assimilated by upper trophic level consumers, though marine-derived C sources dominate. For example, 15 - 70% of polar bear and 0 - 60% of beluga whale carbon was of terrestrial origin. Our results suggest that 1) C_T assimilated by benthic omnivorous invertebrates is transferred to the highest trophic levels in the Beaufort Sea, and 2) arctic cod are the most likely intermediary for transferring C_T from lower to upper trophic levels.

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ABSTRACT

Shallow estuarine lagoons characterize >70% of the eastern Alaskan Beaufort Sea coastline, and like temperate and tropical lagoons, support diverse and productive biological communities. Lagoons experience large variations in temperature (-2 to 14 °C) and salinity (0 to >45) throughout the year. Unlike lower latitudes coastal systems, transitions between seasonal states are physically extreme and event-driven. On high Arctic coastlines, a brief summer open-water period is followed by ice-formation that initiates a nine-month ice covered period, and a late-spring sea-ice breakup coincides with an intense freshwater run-off event. We examined water column structure and inter-annual variations in bottom temperature and salinity at five lagoons that differ in exchange capacity with adjacent marine waters, and magnitude of freshwater inputs over a three-year period (2011-2014). Continuous salinity and temperature measurements from the seabed showed that seasonal transitions in lagoon conditions were filtered by the unique hydrologic and geomorphic characteristics of each lagoon, generating a variety of temperature and salinity (T-S) regimes. Spring break-up and open-water period water column $\delta^{18}O$ and salinity measurements showed that low salinity waters originated from meteoric inputs (e.g., river inputs and direct precipitation) and sea ice melt. Our results suggest that meteoric water is the dominant source of low-salinity water in June and August. Hypersaline conditions that developed during the ice-covered period were largely driven by the degree of lagoon connectivity to Beaufort Sea waters as determined by inlet depth and ice thickness, both of which appeared to vary from year-to-year.

INTRODUCTION

The coastline of the eastern Alaskan Beaufort Sea contains many shallow lagoons, which support productive biological communities (Dunton et al. 2006, 2012). These communities include diverse benthic assemblages that support larger secondary consumers, including marine mammals, water fowl, and fish (Brown 2006, von Biela et al. 2011), which are important resources to the subsistence lifestyle of local Inupiat villages. These lagoons are characterized as estuarine; they can experience large temporal variations in salinity, from almost fresh to hypersaline (McCart 1977). Distinct seasonal changes drive extreme salinity and temperature variations. Resident animals must withstand these fluctuations in order to survive.

Much attention has been given to the potential impacts of climate change on the thermal conditions of Arctic environments (Hinzman et al. 2005), as well as hydrologic change (McClelland et al. 2006, Peterson et al. 2006), but not to how these changes pertain to Arctic lagoon ecosystems. The individual geomorphic and hydrologic characteristics of lagoons may also control their unique salinity and temperature regimes.

While seasonal temperature and salinity patterns in the Arctic are well-documented (McCart 1977, Matthews and Stringer 1984, Hale 1990) the exact timing and duration of transitions among seasons varies from year to year. For example, the spring freshet occurs annually, but the timing and magnitude of peak river discharge varies over time (Carmack and Wassmann 2006, McClelland et al. 2012)**.** The extent that river water overflows landfast ice also varies and can affect the timing of ice breakup (Lissauer et al. 1984). Similarly, the extent of the summer open-water zone can be 1 to 200 km wide (Hale 1990), which will in part modulate the amount of ocean water that mixes into lagoons (Lissauer et al. 1984). Lagoons are affected by wind-generated tidal fluctuations,

which can cause marine water to intrude into lagoons (McCart 1977), so interannual variations in wind conditions will determine the extent of marine influence in lagoons.

Typically, ice formation begins around the end of September (Sellman et al. 1992) and ice cover can reach 2 m thick by April (Barry et al. 1979), with daily accretions of 0.8 to 1 cm (Matthews 1981). For the next nine months, lagoons are ice covered and may freeze completely if depths are largely <2 m. During the sea-ice formation process, the remaining water becomes increasingly saline (35 to >60) due to ion exclusion, allowing hypersaline conditions (i.e. salinities greater than adjacent marine water) to develop in deep areas of the nearshore region and in lagoons (McCart 1977, Hale 1990). Some deep pockets of Simpson lagoon had winter salinities over > 150 (Matthews and Stringer 1984). In contrast, the deeper adjacent waters of the Beaufort Sea, rarely exceed 35 on the sea bed (Sellman et al. 1992)

The spring freshet (associated with rapid snowmelt) typically occurs between late May and early June on Alaska's North Slope (McClelland et al. 2014). Freshwater runoff during this period inundates coastal lagoons and the nearshore environment, accelerating sea ice melt (Pollard and Segar 1994)**.** While the timing (e.g. date of initiation) of the spring freshet varies from year to year, over 50% of annual discharge from rivers on the North Slope occurs during a two-week period each spring (McClelland et al. 2014). The freshet is thought to flush the highly saline brine water out of lagoons (Hale 1990) and during this time, lagoons experience drastic fluctuations in both temperature and salinity. Lagoons tend to be stratified with respect to salinity and temperature because warmer, less saline river water flows under the local sea ice and sits on top of cooler, more saline waters (Dunton et al. 2006). Tidal mixing is negligible and ice-cover prevents wind-mixing, so this stratification persists until the remaining local sea ice melts.

Lagoons are normally ice-free by early July. Melting is accelerated by stream water overflowing ice, which both increases the temperature and decreases the albedo (Schell et al. 1984). During the summer open-water period, freshwater inputs decrease (becoming insignificant by early fall) and wind-driven mixing increases. These changes destabilizes lagoon water column stratification allowing complete vertical mixing (Schell et al. 1984). Winds and tides also advect marine water into lagoons further contributing to water column mixing (Hale 1990).

Both river runoff and sea ice melt deliver low-salinity water to lagoons and the nearshore environment each spring (McClelland et al. 2012), but the relative importance of these freshwater sources is not well described for much of the Arctic coast. Salinity and water column oxygen isotopic ratios (H_2O-$\delta^{18}O$) are reliable tracers of freshwater sources (i.e. sea ice melt vs. runoff) that enter lagoon environments. This method has been used extensively in the Arctic (Ostlund & Hut 1984; Macdonald et al. 1989; Cooper et al. 1997; Cooper et al. 2005).

The accuracy of the H_2O-$\delta^{18}O$ approach to identify source waters continues to improve as oxygen isotope end-member values become more refined (Cooper et al. 2005; Cooper et al. 2008; Yi et al. 2012)**.** Arctic sea ice is typically -2.4‰, which is ~1‰ more enriched than seawater (~-3.5‰) (Macdonald et al. 2002, Cooper et al. 2005, Alkire and Trefry 2006). Arctic rivers integrate meteoric precipitation from the preceding winter, and are characterized by highly depleted H_2O-$\delta^{18}O$ values (-15 to -22‰ depending on region) relative to seawater (Cooper 1998, Cooper et al. 2008). Determining the main source of low-salinity water in lagoons may help researchers predict how lagoon salinity regimes will be affected by changes in runoff and sea-ice dynamics.

Several lagoons along the eastern Alaskan Beaufort Sea coast were the subject of research led by the U.S. Fish and Wildlife Service investigators in the 1970s and 1980s

(Schell et al. 1984, Hale 1990, 1991, Pollard and Segar 1994). These studies focused on spring and summer dynamics. However, there is nearly a complete lack of information on the hydrography of these lagoons during the ice-covered period due to the difficulty of access.

This study aims to provide baseline hydrographic information for characteristic coastal lagoon ecosystems in the eastern Alaskan Beaufort to enable better understanding of a system that is projected to change significantly with respect to precipitation, land runoff, sea ice melt, and storms surges (Chapin 2005, Hinzman et al. 2005, Peterson et al. 2006). We examined the salinity and temperature regimes of five representative lagoons and embayments along the eastern Alaskan Beaufort Sea coast using continuously recording *in situ* sensors. Discrete measurements were also made during field trips covering three distinct seasons — winter ice-cover (April), spring breakup (June), and summer open-water period (August) — during 2011-2014. All five lagoon systems varied in their geomorphology, degree of connectivity to nearshore marine waters, and magnitude of freshwater inputs.

Our main objectives were to *1)* determine seasonal patterns, including the ice-covered period, in water column structure at each lagoon system, *2)* characterize interannual variability in lagoon temperature and salinity, as well as determine the timing of key hydrologic events, *3)* quantify the proportion of low-salinity water present in lagoons during spring and summer that originates from sea ice melt vs. meteoric water, and *4)* determine how differences in lagoon geomorphology, exchange properties, and freshwater inputs modulate seasonal patterns and interannual variability in temperature and salinity.

METHODS

Regional Setting

The Alaskan Beaufort Sea-shelf is ~80 km wide and is characterized by a discontinuous chain of barrier islands which enclose coastal lagoons (**Fig. 1.1**). The Beaufort coast is characterized by mixed, semi-diurnal tides (10-30 cm), which have little effect on nearshore circulation but can be important to lagoon mixing (Lissauer et al. 1984, Hale 1990). Storm surge events, while rare, usually occur in early fall and can increase sea level up to 3 m (Wise et al. 1981, Kowalik 1984). Storm surges and wind driven currents both enhance exchange between lagoons and nearshore waters (Schell et al. 1984).

Prevailing winds blow from the northeast over the Beaufort Sea, resulting in the Beaufort Gyre; this current flows east to west along the shelf and experiences current speeds up to 3-4% of the wind speed (Matthews 1980). The Beaufort Undercurrent flows in the opposite direction, west to east, along the continental slope carrying water of Pacific and Atlantic origin (Pickart 2004). Wind-driven upwelling can cause cooler, more saline, and more nutrient-rich water from the Beaufort Undercurrent to intrude into lagoons (McCart 1977, Macdonald et al. 1987). The direct effects of winds depends on lagoon stratification – during strong winds weakly stratified lagoons mix and respond as one water mass, whereas in highly stratified lagoons only the surface layer experiences increases in horizontal velocity (Hale 1990). Since lagoons are generally more stratified in early open-water period, wind mixing of the entire water column occurs mostly in late summer.

Several large rivers such as the Colville and Mackenzie, deliver freshwater to the Beaufort Sea during late spring and summer (Macdonald et al. 2004). Smaller rivers and tundra streams (discussed below) are also important sources of freshwater at a more

localized scale. The large volume of freshwater inflow to lagoons and the inner shelf contribute to the characterization of the southern Beaufort Sea as an estuarine environment during the summer open-water season (Dunton et al. 2006, McClelland et al. 2012).

Field Sites

This study focuses on five lagoon/bay systems along the eastern Alaska Beaufort Sea coast – Kaktovik, Jago, Angun, Nuvagapak, and Demarcation (**Figs. 1.1, 1.2**). Although these systems are located within 100 km of each other, each lagoon is unique in size, shape, freshwater inputs, and connections to nearshore waters. All lagoons are fully ice covered in the winter months, although, none freeze completely to the bottom except along their perimeters to depths of 1.8 m. Lagoon systems were still partially ice covered during June 2012 and 2013.

Kaktovik Lagoon (KA; **Fig. 1.2a**), the westernmost study system, is almost fully enclosed by Barter Island (on which the village of Kaktovik is located) to the west, a peninsula from the mainland to the east, and barrier islands to the north. KA is 3 - 4 m in depth, with deeper areas near the southern land margin and shallower areas near the northern barrier islands. KA receives relatively small amounts of freshwater input from small tundra streams and diffuse runoff (Dunton et al. 2012). The nearest named rivers are 9 km to east (Jago River) and 13 km to west (Hulahula River) (McCart 1977). KA is not connected directly to the Beaufort Sea, but is connected to other lagoon systems via two channels. Nelsaluk Pass (~3 m deep) in the northeast corner connects KA to Jago Lagoon, and a minor channel (<1 m deep) in the southwest corner of the lagoon connects KA to Arey lagoon (Hale 1990). KA is thought to experience continuous mixing during the open-water period (McCart 1977).

Jago Lagoon (JA; **Fig. 1.2a**) is directly east of KA; a peninsula that connects to the mainland separates the two lagoons (Hale 1990). In addition to the small channel connection to KA, JA is connected to the Beaufort Sea by two large channels. The largest channel is a 3 km wide, 1 m deep connection in the mid-lagoon between Bernard spit and Jago spit known as Jago Entrance, and the other channel is north of Barter Island. JA receives direct freshwater inputs from the Jago River in the east, as well as a few small tundra streams in the west. The JA system connects with Tapkauruk Lagoon east of the Jago River.

Angun Lagoon (AN; **Fig. 1.2b**), the smallest study system, is located 30 km east of JA. AN is long and narrow and is mostly separated from the open ocean by sand spits. This lagoon is shallow (2.5 - 3.5 m deep) and is connected to the Beaufort Sea by three small channels (< 0.5 km wide, ~2 m deep) in the northeast section of the lagoon. Three small rivers (the Angun and Siktelurak in the east and Sikuik in the west) empty directly into AN.

Nuvagapak Lagoon (NU; **Fig. 1.2b**) is 5 km further east of AN, and is approximately twice the size of AN, but is also long and narrow in shape. NU is shallow (~3 m in depth), with mostly flat bathymetry. It is semi-enclosed, and receives inputs from small rivers and streams, including the Alchilik in the east and the Kogotpak in the middle. NU has one large connection to marine waters, a 1 km wide, 1.3 m deep channel in the northwest corner, and one small channel (< 1 m deep) in the northeast corner east of the Alchilik River.

Demarcation Bay (DE; **Fig. 1.2c**), is located furthest east, about 40 km east of NU. DE is the largest and deepest study system. Its only connection to the Beaufort Sea is via one large and relatively deep channel (1 km wide). DE is shaped like a typical embayment as opposed to the longer, narrower shape of the other lagoon systems. DE is

3 m deep on average, with deeper areas (4.5 m) in the center of the bay and shallower (3 - 3.5 m) areas near all land margins. Two small tundra streams enter the bay on the SE and SW corners. The bay is also connected to a long, narrow lagoon (Pingokraluk Lagoon) to the northwest via a shallow (0.5 m deep) channel.

Field Methods

During August 2011, HOBO U24 Conductivity Loggers (U24-002-C) were deployed at two stations within each lagoon (KA-A, KA-B, JA-A, JA-B, AN-A, AN-B, NU-A, NU-B, DE-A and DE-B) approximately 30 cm above the seafloor (**Fig. 1.2**). Each logger was placed in a PVC housing and secured to a line that was anchored and connected to a buoy approximately 25 cm above the sea floor to maintain correct orientation. The loggers recorded conductivity and temperature (with a resolution of ±2 $\mu S\ cm^{-1}$ and 0.01 °C respectively) in 2-hour intervals. They were retrieved and downloaded several times throughout the study period between August 2012 and August 2014 (**Table 1.1**). We could not retrieve the AN and NU loggers at the end of the study period due to dangerous weather and sea conditions.

Logger Data

Upon retrieval, HOBOware Pro (v.3.7) software was used to download the data and HOBOware Conductivity Assistant (v.2.4) was used to convert conductivity measurements to salinity based on the Practical Salinity Scale 1978 (PSS-78). Salinity sensors failed on the DE-B logger and on the KA-A logger in the final year, and this data is excluded from our analysis. The remaining loggers exhibited some drift in measurements following exposure to low-salinity water. To correct for this drift, the data were calibrated using YSI sonde measurements. A two-point calibration was determined for each lagoon. For KA, JA, and AN loggers, sonde conductivity and temperature

measurements collected from 3 m at stations A and B in April 2012 and 2013 were used as the two calibration endpoints. For NU loggers, 3 m sonde measurements were applied from data collected in August 2011 and April 2012. For DE loggers, we applied 3 m sonde measurements from August 2011 and August 2012. The resulting salinity record closely matched (±3) sonde salinity records from each station.

Additional data were collected during sampling trips to the lagoons in April, June, and August over a three-year period (**Table 1.2**). Stations were accessed by snow machine in April and aboard the *R/V Proteus* during the August open-water period. During June sampling trips, we landed on barrier islands or sand spits near each lagoon in a fixed wing Heliocourier, and then used an inflatable boat to access each station. Two stations were sampled in April and June, while two or three stations were sampled in August when lagoon waters were more accessible by boat. Pre-selected stations were located using a GPS with an accuracy of 4 m or better. Each station was designated as the area within a 10 m radius of the GPS location.

During each sampling trip, hydrographic measurements including water depth, conductivity/salinity, and temperature were collected at each station with a YSI 600XL data sonde. Measurements were recorded for surface, bottom, and mid-water column at 1 m intervals. During April sampling, sonde measurements were recorded at 2 m and 3 m to account for an ice thickness that averaged about 1.7 m.

Water samples were also collected for H_2O-$\delta^{18}O$ analysis in 30 ml HDPE sample bottles. These samples were collected using a peristaltic pump from 1 (August only), 2, and 3 m below the surface. Sample bottles were filled completely and stored unfrozen until analysis. These samples were analyzed at the Stable Isotope Laboratory at the Marine Biological Laboratory in Woods Hole, MA with a precision of 0.02 ‰.

Source Water Partitioning

We quantified the proportion of lagoon water that originated from sea ice melt (SIM) and runoff/ meteoric water (MW) using a model that assumes these sources mix with marine waters derived from the Polar Mixed Layer (PML; Alkire & Trefry 2006). We estimated the percent contribution from each of these three sources (SIM, MW, BW) by simultaneously solving the following three equations for all water samples:

Equation 1: SIM + MW + PML = 100

Where SIM, MW, and PML are the percent of water originating from each source.

Equation 2: S = (SIM x 5) + (MW x 0) + (PML x 31.6)

Where S is salinity of the water sample and each fraction is multiplied by its assumed salinity.

Equation 3: $\delta^{18}O = (-2.4‰ \times SIM) + (-22.0‰ \times MW) + (-3.5‰ \times PML)$

Where $\delta^{18}O$ is the stable oxygen isotope value of the water sample and each fraction is multiplied by its assumed $\delta^{18}O$ value.

This model relies on assumptions about the $\delta^{18}O$ values of the three end-members. We assigned a $\delta^{18}O$ value of -22.0‰ for MW because small Arctic rivers that drain in the Brooks Range on Alaska's North Slope tend to be slightly more depleted than larger rivers (Cooper et al. 2005**,** McClelland unpublished data). Similar to the end-members used by Cooper et al. (2005), we use -2.4‰ for SIM (Eicken et al. 2002) and -3.5‰ for PML (Alkire and Trefry 2006). These equations produced negative values for SIM and PML in a small number of cases, which is likely an artifact of the variability in true end-member values.

RESULTS

Water column structure

The April ice-cover conditions within lagoons did not vary between years or within lagoons, though there were slight differences in maximum salinities among lagoon systems. Water temperatures ranged from -1.6 to -2.1 °C (**Fig. 1.3**). KA and NU had surface (≤ 2 m) salinities over 40, whereas JA and AN were less saline at 31-35. Salinities at or below 3 m were consistently greater (by 2-5) than salinities measured at ≤ 2 m, as well as greater than salinities in the PML.

During late June (ice break-up period), results were more variable among years and lagoons (**Fig. 1.3**). All lagoons were ~5°C warmer in June than in April, and all lagoons except for AN were strongly stratified with respect to salinity at one or more sampling locations. Waters ≤ 2 m generally had salinities between 2 and 4 during June, with the exception of NU, where saltier water was occasionally encountered near the surface. Salinities of deeper waters (≥ 3 m), on the other hand, differed widely among lagoons, with KA showing consistently high values, AN showing consistently low values, and JA and NU showing a mixture of low and high values. The variability in bottom water salinities at JA during June reflects differences among sampling sites, whereas the variability in bottom water salinities at NU reflects differences among years (stratified during June 2012, but not in June 2013). There was also a negative temperature gradient of 2-5°C from surface to bottom water at KA, JA, and NU during June.

Stratified conditions were maintained at some locations during August, but differences between surface and deep water samples were less consistent among lagoons and between years than observed during June (**Fig. 1.3**). All lagoons had substantially warmer (> 8°C) and more saline surface waters in August than in June. In 2012, KA and NU still contained highly saline bottom water and were thus stratified with surface and

bottom salinities of ~20 and ~38 (KA) and ~4 and ~30 (NU), respectively. In 2012, JA and AN were well mixed with respect to salinity. Though data from both years is combined in Fig. 3, water column structure in 2013 was substantially different than in 2012—KA, JA, and AN surface waters were 2 to 6 °C warmer than in 2012 and were stratified with respect to temperature. Salinity was relatively constant with depth in KA, and only increased by 4 with depth in JA and AN.

Sonde data were only collected from DE during August 2012. Three stations were sampled; temperature was uniformly 9-11 °C in surface and bottom waters, and salinity varied from12-15 in surface waters to 23 in bottom waters.

Seasonal and interannual variation in bottom water parameters from moorings

All lagoons showed the expected seasonal patterns in temperature and salinity, though there were differences among lagoons and between years (**Fig. 1.4**). Minimum temperatures (~-2.0 °C) were reached by mid-October in KA, JA, and AN; by early-November in NU; and in late-November in DE, a pattern which held true over all sampling years. As temperatures cooled during each ice-cover season, hypersaline conditions (>PML salinity) developed in most lagoons. KA and NU stations were the most saline (>40), followed by JA, AN and DE never reached 40. Maximum salinities during the ice-cover months were somewhat lower in 2013/14 relative to the two earlier ice-covered seasons. This decrease was observed at all lagoons for which three years of data was available, but was less pronounced at JA (5 decrease at JA-A, 2 increase at JA-B) than at KA (KA-A: 10 decrease, KA-B: 6 decrease) or DE (DE-A: no change, DE-B: 6 decrease).

Salinity patterns during the winter ice-covered period different among lagoons and years. KA sites continued to increase in salinity during the entire ice-covered period

during every year for which data is available. Conversely, DE-A salinities plateaued around December each year, and remained ~36 until the spring freshet. NU behaved similarly to KA in winter 2011/2012. JA and AN, however, showed both patterns depending on the year. In 2011/2012 both JA and AN stations plateaued similar to DE-A, but in 2012/2013 their salinity increased throughout the ice-cover period, similar to KA stations.

Low salinities and warm temperatures that fluctuated widely characterized the summer open-water period. KA-A, JA-B, NU-A, and both DE stations experienced the most variation in hydrographic parameters during the summer. Minimum open-water salinities varied between lagoon stations, sampling years, and among lagoons, with only two stations (KA-A and DE-A) ever becoming entirely fresh (0; **Fig. 1.4**). Both KA, JA, and AN stations reached lower minimum salinities in summer 2013 than in summer 2012. Though KA-B, JA-A, and AN-A (2012 only) experienced the same temperature increase as other stations, their salinity did not decrease below 20. In late August, temperatures at all lagoons began to decrease again and salinities began to increase.

The annual ranges in temperature and salinity varied among lagoons and years. In general, low salinities are associated with high temperatures and vice versa (**Fig. 1.5**). Most of the observed ice-covered values fall on the freezing point curve of the TS scatterplot, which provides one indication that the HOBO loggers maintained their calibrations through the ice-covered period.

Source water partitioning

The seasonal patterns in H_2O-$\delta^{18}O$ and salinity were consistent across all lagoon systems and provided information on the contribution of marine water and two sources of low-salinity water to each lagoon (**Table 1.3, Figs. 1.6, 1.7**). In April, lagoon waters were

consistently hypersaline, and enriched in ^{18}O, which corresponded to large contributions of PML from the Beaufort Sea (>80%) and minor meteoric water contributions (<20%). Little to no sea ice melt water was present in lagoons in April. No differences were observed among sampling depths in April.

In June, most lagoons contained low-salinity water (<6) that was depleted in ^{18}O (<-10‰), with small and variable contributions of PML water (**Figs. 1.6A, 1.7**). MW was the main source of freshwater inputs at all lagoons, accounting for at least 50% of water in surface layers on all lagoons. SIM also contributed significant amounts of water to all lagoons. PML was only present in bottom layers of KA, JA, and NU. Three samples from KA and two from JA, all of which were collected from 3 m, were more saline (>30) and were ^{18}O enriched than other June samples (**Fig. 1.6A**). These were likely winter water that was not fully flushed from these lagoons in June. One sample from KA and two from NU were more saline (25 - 45) but had similar $\delta^{18}O$ values to the majority of June samples, which likely indicate the presence of low-salinity water in lagoons during freeze-up, which became hypersaline from ion-exclusion but retained their depleted $\delta^{18}O$ value.

August samples span a wide range in salinity (5-30) and $\delta^{18}O$ values (-20 to -5‰), which corresponded to greater contributions of marine water to all lagoons (40 to 70%) than in June (**Figs. 1.6B, 1.7**). Deeper samples ($\geq$ 3 m) were more saline and more enriched in ^{18}O than most 2 m samples, though 1 m samples spanned the entire range. MW was the dominant source (30 - 50%) of low-salinity water at all lagoons, though small amounts of sea ice melt water (5-30%) were present in most lagoon stations. NU contained more low salinity water than all other lagoons.

DISCUSSION

The winter ice-covered period

Waters in all the lagoons began to freeze by late September and were covered by 1.5-2 m of ice by April in 2012 and 2013. Under-ice waters were uniformly cold, saline, and similar in $\delta^{18}O$ composition to the adjacent Beaufort Sea waters. The Polar Mixed Layer is a major source of water in these lagoons, largely due to mixing during the previous open-water period and, in some cases, under ice exchange (Lissauer et al. 1984). The winter water column structure remained stable throughout the iced-over period since waters are highly insulated from meteorological events.

Lagoons varied in their salinity regimes during the ice-covered period. Some lagoons plateaued at lower salinities around December, whereas other lagoons continued to develop hypersaline conditions until the spring freshet. These trends are likely modulated by exchange with adjacent nearshore waters. Lagoons with appreciable exchange with nearshore waters did not become hypersaline, as marine source waters (PML) continually modulated their salinities. KA, which has no direct channels to marine water, developed hypersaline conditions every winter, whereas DE, which has a large opening to marine waters, appears to maintain exchange during every winter. JA and AN showed different salinity regimes depending on the year, possibly because exchange channels froze completely during some years. Previous studies on AN speculate that currents running through the lagoon channels are strong enough during the ice-cover months to prevent brine water from accumulating to the extent observed in more closed lagoons (Schell et al. 1984).

The spring breakup period

In late spring, lagoons were still partially ice-covered and experienced a period of rapid warming and freshening caused by the spring freshet, This large inflow of freshwater floats above more saline water (Dunton et al. 2006), causing the stratification observed in sonde cast data and in source water (i.e. PML only present in bottom waters).

A more saline bottom layer that was also a few degrees cooler than overlying water was present in KA, JA, and NU, but not AN. This bottom layer was likely the remnants of brine buildup from the previous winter and not the result of marine intrusion, because it had higher salinities than the nearshore Beaufort Sea (Schell et al. 1984, Hale 1990). While AN also contained high salinity water in April, this system, which is small and received inputs from several streams, was likely flushed before our June sampling in both years. In 2013, however, NU was also brine free in June, suggesting NU was flushed earlier in 2013 than in 2012.

A 1982 study similarly observed that AN did not contain a brine layer in late July, though NU did, and reported that AN's water column became well-mixed several weeks after ice out (Schell et al. 1984). Hale (1990) found similar patterns, but with different timing, in 1988. KA was brackish (~13) with 1.5 semidiurnal fluctuations in early June. During our sampling years, 3 m waters were reaching their maximum salinities in early June (>30). By late June when sonde cast data were collected, the surface waters of all lagoons had freshened (2-22), but still contained deeper brine pools (42) below 3 m. This suggests that breakup occurred later during our sampling years than in 1988.

Eventually freshwater from the freshet mixes to deeper lagoon waters, when we observe freshening in the HOBO logger data (i.e. near 0 salinities at DE stations, which were sustained for several weeks before increasing to 30). Though low-salinity water entered and freshened all lagoons, we observed differences in the magnitude of these

inputs among lagoons. In late June, all lagoons contained only water from freshwater sources (except bottom waters at KA, JA, and NU, which contained PML). This demonstrates how quickly large volumes of water can inundate these shallow lagoons. Surprisingly, JA, which had the greatest amount of freshwater inflow (not counting DE, which was not sampled in June), did not contain the most MW. These differences may be explained by varying rates of river inputs. SIM was an important freshwater source (<30%) to all lagoons in June. KA and NU did not contain sea ice melt water. As expected, KA, which had no direct river inputs, contained the least MW and the most SIM. Our results differ from previous work in KA and JA, which concluded these lagoons contain significant amounts of coastal water in early June (Hale 1990, 1991).

The summer open-water period

During the open-water period, all lagoons were flushed of hypersaline water that accumulated during the ice-covered months, though the timing of flushing differed among lagoons and between years. In August 2012, KA and NU contained hypersaline bottom waters, but these lagoons had been flushed completely by August 2013, which contributes to the large variation in bottom water salinity seen in Fig. 3. KA was probably flushed the slowest of all the lagoon sites because it has minimal direct freshwater inputs (Hale 1990). Hale (1990) also observed that JA was flushed of brine water by mid-July in 1988, presumably due to freshwater inputs from the Jago River.

By August, marine waters had intruded into all lagoons, resulting in greater proportions of PML water than in June, though there was slight variation among lagoons. These variations seemed to be driven by differences in freshwater inputs rather than by circulation patterns. One or a combination of the following reasons may explain the differences between JA and NU: 1) JA had a much larger entrance to the Beaufort than

NU, which may allow more marine water to enter, 2) more mixing was typically observed in "bay" shaped lagoons, like JA, than narrow lagoons (Lissauer et al. 1984), and/or 3) meteoric waters were more important in NU because it did not have another lagoon on its eastern side to dilute river inputs, as did JA (Tapkaurak lagoon).

In regards to August water column structure, all lagoons had uniform salinity, which likely indicates the deep brine layer observed in KA and JA in June was flushed before August sampling occurred. Our 2012 results for KA and 2013 results for JA were similar to previous observations at these lagoons. Hale (1990), reported that KA and JA were stratified during the open-water period, but layers in JA could be distinguished by temperature, and layers in KA could be distinguished by salinity (12-35 in KA vs. 12-13 in JA). While JA had uniform salinities throughout the water column, we found it to be consistently more saline (22).

Once ice free, water exchange rates between the open ocean and lagoons (except KA which only receives inputs from other lagoons) increase (Hale 1990). Water from the open ocean mixes with the low-salinity water, and all lagoons contain a greater proportion of PML water and less water from low-salinity sources in August than in June. On average, sea ice melt comprised 10% of water at all lagoons. All lagoons became increasingly saline over the summer and salinity and temperature variation decreased as the open-water period progressed. This pattern was likely caused by a combination of marine intrusion, wind mixing, and decreasing air temperatures (Hale 1990, 1991).

The end of the open-water period and start of freeze-up was indicated by dropping temperatures in late September to October, which occurred at the same time as in the 1970s (McCart 1977). KA and NU only had inputs from small tundra streams whereas DE, AN, and JA all had direct river inputs from one or more rivers.

Conclusions

Although the five representative eastern Alaskan Beaufort Sea lagoon systems were subjected to similar meteorological conditions during the three-year study period, we observed differences in temperature and salinity regimes and source water contributions, and the timing of seasonal events among lagoons. These differences illustrated that the unique hydrology and geomorphology of each lagoon modulated its regime. These differences appear to be driven primarily by differences in exchange with nearshore waters.

For example, small lagoons with high freshwater inputs, like AN, were flushed of brine water in the open-water period more rapidly than larger lagoons with fewer freshwater inputs, like KA and JA. Also, lagoons like KA and NU that have less exchange with marine waters, continued to develop hypersaline conditions throughout the ice-cover period.

Exchange rates with marine waters caused most of the variation among lagoons. This is, in part, modulated by rates of freshwater inputs, so global warming may cause significant changes to the hydrologic dynamics within Arctic lagoons. Rising Arctic temperatures are predicted to alter precipitation, runoff, and stream flow on Alaska's North Slope (Hinzman et al. 2005, Peterson et al. 2006), which may increase low-salinity water inputs. The duration of the open-water period is also predicted to increase, as is storm frequency and intensity, which would increase marine intrusion into all coastal lagoons (Hinzman et al. 2005). The effect of these phenomena on resident lagoon faunal communities or on summer migratory animals is currently unknown.

Future research should quantify the amount of freshwater inputs each lagoon receives as well as the amount of exchange that occurs through the lagoon channels at various times of the year. Measurements of circulation would also help

calculate residence times of Beaufort Sea lagoons. This will help provide better insight into how regional changes in climate and its associated effects on freshwater inflow and the timing of freeze-up and break-up may impact lagoon ecosystems.

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Table 1.1 Record of HOBO logger deployment, mid-study downloads, and retrieval. Loggers in Angun and Nuvagapak were never retrieved due to dangerous weather and sea conditions.

Logger	Deployment	Download(s)	Retrieval
KA-A, KA-B	Aug 2011	Aug 2012, Aug 2013, April 2014	April 2014
JA-A, JA-B	Aug 2011	Aug 2012, Aug 2013, April 2014	April 2014
AN-A, AN-B	Aug 2011	Aug 2012, Aug 2013	N/A
NU-A, NU-B	Aug 2011	Aug 2012	N/A
DE-A, DE-B	Aug 2011	Aug 2012, May 2013	May 2014

Table 1.2 Location, maximum depth, and years sampled for five lagoons along the Alaskan eastern Beaufort Sea.

Site	Station	Latitude (°N)	Longitude (°W)	Max Depth (m)	Years Sampled
Kaktovik	KA-1	70.086	-143.614	3.5	2011, 2012, 2013
	KA-2	70.101	-143.578	3.7	2011, 2012, 2013
	KA-3	70.118	-143.570	3.2	2011, 2012, 2013
	KA-4	70.109	-143.599	3.7	2012, 2013
	KA-A	70.089	-143.623	3.0	2012, 2013
	KA-B	70.101	-143.571	3.0	2012, 2013
	KA-K	70.124	-143.583	3.5	2012, 2013
Jago	JA-1	70.106	-143.503	3.5	2011, 2012, 2013
	JA-2	70.110	-143.427	3.5	2011, 2012, 2013
	JA-3	70.116	-143.379	2.0	2011, 2012, 2013
	JA-4	70.105	-143.463	3.5	2012, 2013
	JA-A	70.107	-143.443	3.0	2012, 2013
	JA-B	70.104	-143.489	3.0	2012, 2013
Angun	AN-1/ AN-A	69.959	-142.494	3.5	2011, 2012, 2013
	AN-2/ AN-B	69.948	-142.440	3.2	2011, 2012, 2013
	AN-3	69.943	-142.434	3.2	2012, 2013
	AN-4	69.942	-142.445	2.5	2012, 2013
Nuvagapak	NU-1	69.86	-142.19	3.0	2011, 2012
	NU-2	69.88	-142.24	3.0	2011, 2012
	NU-3	69.90	-142.31	3.0	2011, 2012
	NU-4	69.87	-142.20	3.0	2011, 2012
	NU-A	69.88	-142.25	3.0	2011, 2012
	NU-B	69.90	-142.32	3.0	2011, 2012
Demarcation	DE-1/ DE-A	69.634	-141.267	2.5	2011, 2012
	DE-2/DE-B	69.660	-141.340	4.0	2011, 2012
	DE-3	69.683	-141.413	3.0	2011, 2012

Table 1.3 H_2O-$\delta^{18}O$ (mean ± SE (n)) for depths where oxygen isotope samples were collected during each samples season.
Values are averages across all sampling years and stations. A dash (-) indicates data were not collected.

Site	$\delta^{18}O$ (‰)		
	April (28)	**June (34)**	**August (61)**
Kaktovik	**-4.2 ± 0.2 (6)**	**-10.0 ± 1.9 (8)**	**-6.8 ± 0.2 (19)**
1 m	-	-	-5.7 ± 0.1 (3)
2 m	-4.1 ± 0.2 (4)	-13.4 ± 0.8 (4)	-7.2 ± 0.3 (8)
3 m	-4.5 ± 0.1 (2)	-6.6 ± 2.8 (4)	-6.9 ± 0.4 (8)
Jago	**-3.6 ± 0.2 (8)**	**-13.5 ± 1.6 (10)**	**-6.0 ± 0.3 (13)**
1 m	-	-	-5.5 ± 0.6 (3)
2 m	-3.4 ± 0.1 (4)	-16.3 ± 0.7 (6)	-6.5 ± 0.5 (6)
3 m	-3.8 ± 0.3 (4)	-9.3 ± 2.9 (4)	-5.7 ± 0.7 (4)
Angun	**-3.4 ± 0.1 (8)**	**-16.8 ± 0.6 (7)**	**-6.5 ± 0.7 (10)**
1 m	-	-	-4.6 ± 0.1 (2)
2 m	-3.3 ± 0.1 (4)	-16.7 ± 0.9 (4)	-7.2 ± 1.2 (4)
3 m	-3.5 ± 0.1 (4)	-16.8 ± 0.8 (3)	-6.9 ± 1.3 (4)
Nuvagapak	**-4.3 ± 0.2 (6)**	**-16.8 ± 1.2 (9)**	**-11.4 ± 1.7 (11)**
1 m	-4.2 ± 0.4 (3)	-19.5 ± 0.9 (4)	-13.8 ± 2 (5)
2 m	-4.4 ± 0.3 (3)	-14.6 ± 2 (4)	-13.3 ± 3.6 (3)
3 m	-	-	-5.5 ± 0.1 (3)
Demarcation	**-**	**-**	**-6.7 ± 1 (8)**
1 m	-	-	-4.1 ± 0.4 (3)
2 m	-	-	-9.6 ± 1.5 (3)
3 m	-	-	-6.1 ± 0.6 (2)

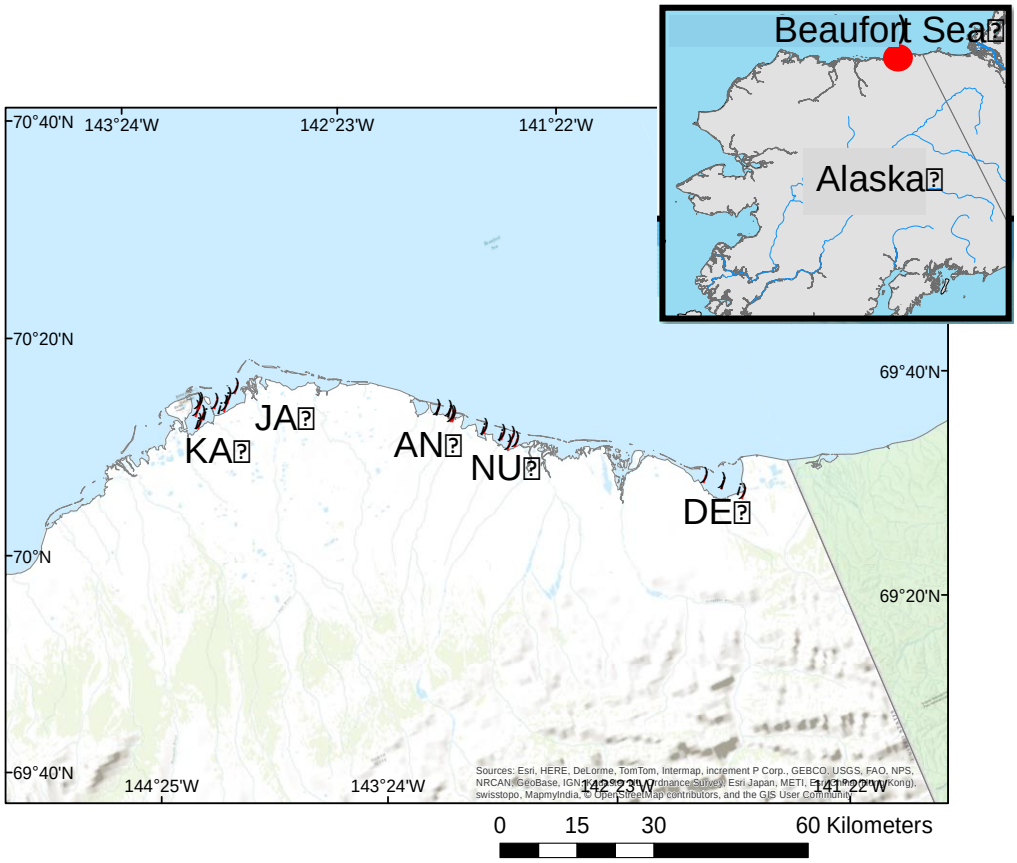

Figure 1.1 Site locations within each lagoon along the coast of the Alaskan Beaufort Sea that were sampled in April, June, and August of 2011-2013.
See Table 1.2 for station code definitions. In each lagoon, temperature and salinity loggers were deployed in August 2011 (black circles), temperature and salinity profile data was obtained using a YSI data sonde (red circles), and water samples were collected for H_2O-$\delta^{18}O$ analysis.

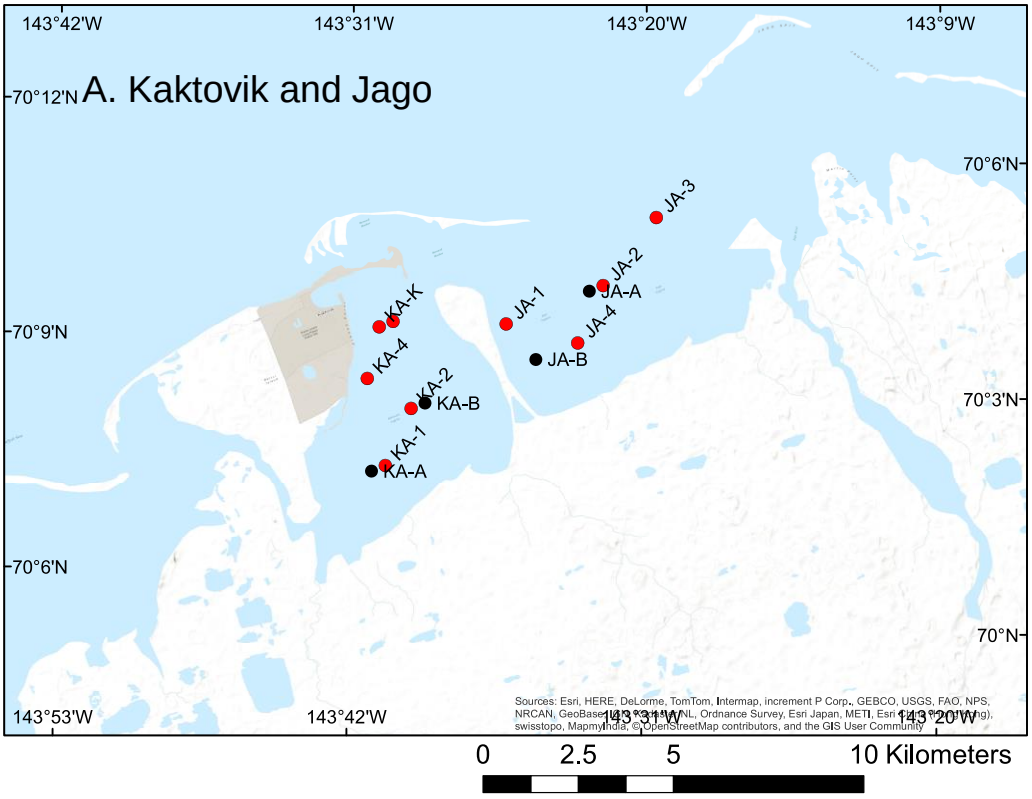

Figure 1.2A Site of HOBO loggers deployment (lettered stations, black circles) and data sonde profiles (numbered stations, red circles) in Kaktovik and Jago Lagoons.

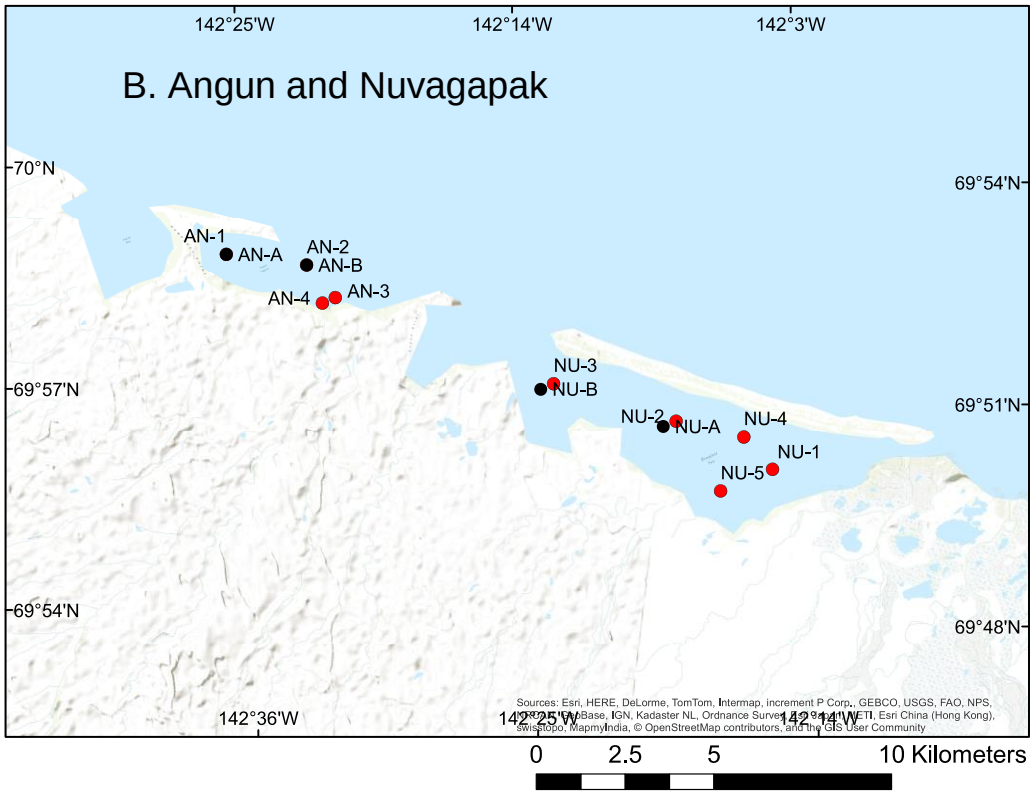

Figure 1.2B Site of HOBO loggers deployment (lettered stations, black circles) and data sonde profiles (numbered stations, red circles) in Angun and Nuvagapak Lagoons.

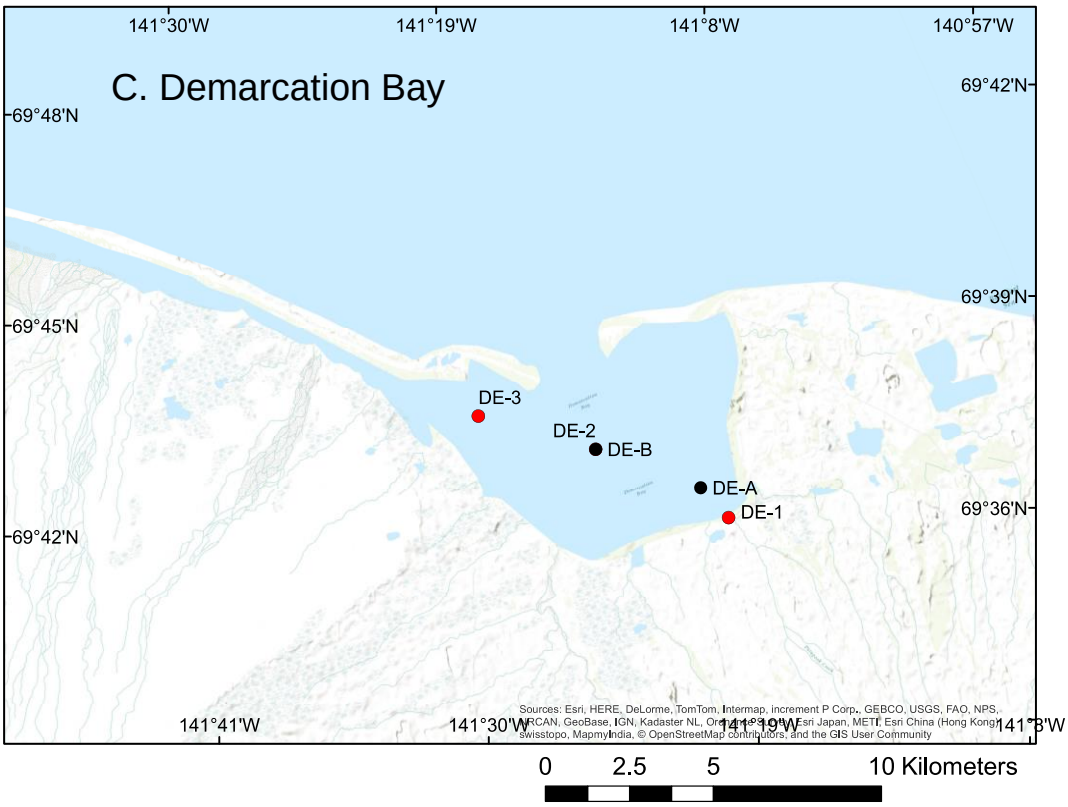

Figure 1.2C Site of HOBO loggers deployment (lettered stations, black circles) and data sonde profiles (numbered stations, red circles) in Demarcation Bay.

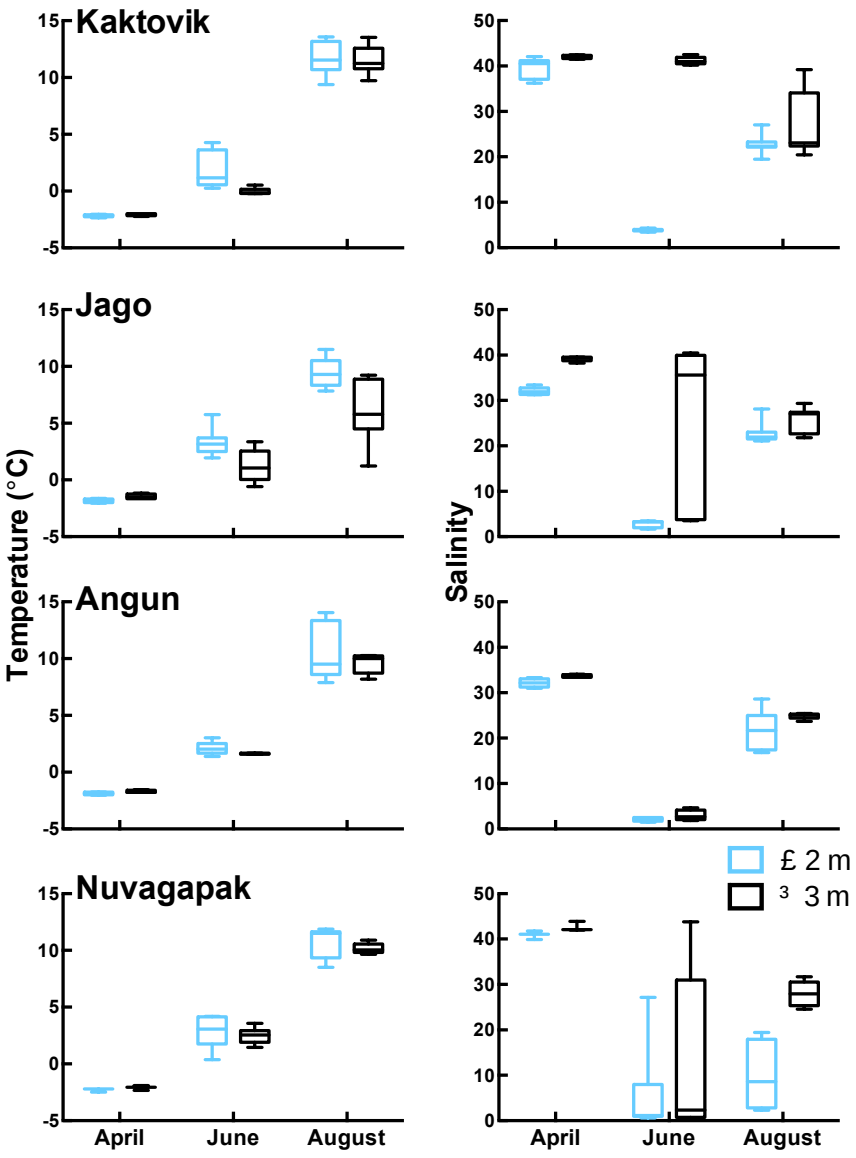

Figure 1.3 Temperature and salinity of surface waters (≤ 2 m) and bottom waters (≥ 3 m) from YSI data sonde casts for several stations at each lagoon during April (winter ice-cover), June (spring breakup) and August (summer open-water period). Data from all years and all stations is included. Demarcation Bay was only visited during August, data is not show here.

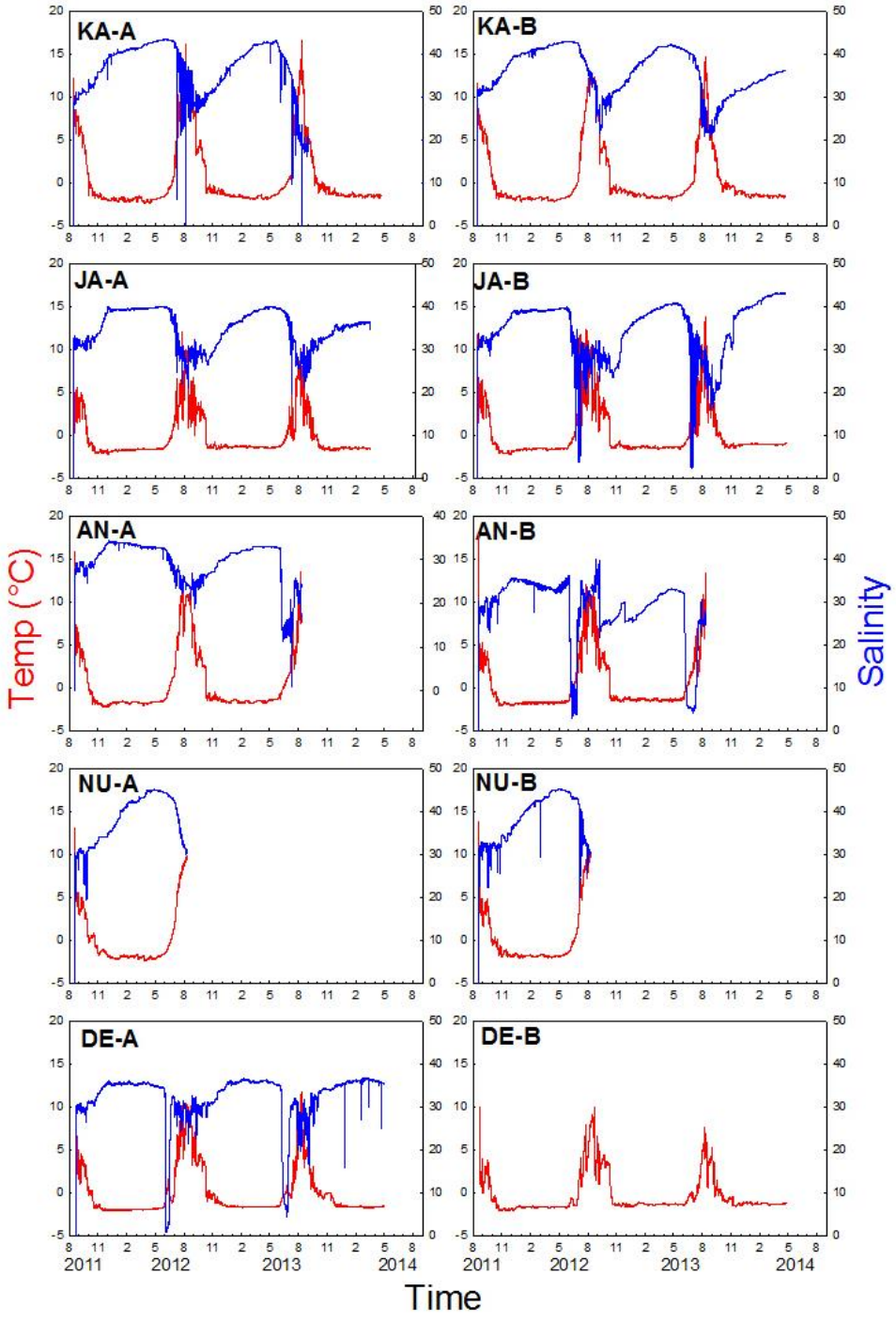

Figure 1.4 Salinity and temperature data for two stations (A and B) within each lagoon obtained from HOBO loggers. Salinity was calculated based on conductivity and temperature data using PSS-78 conversions and calibrated with YSI sonde measurements (see methods for more details). Months are numbered on x-axis.

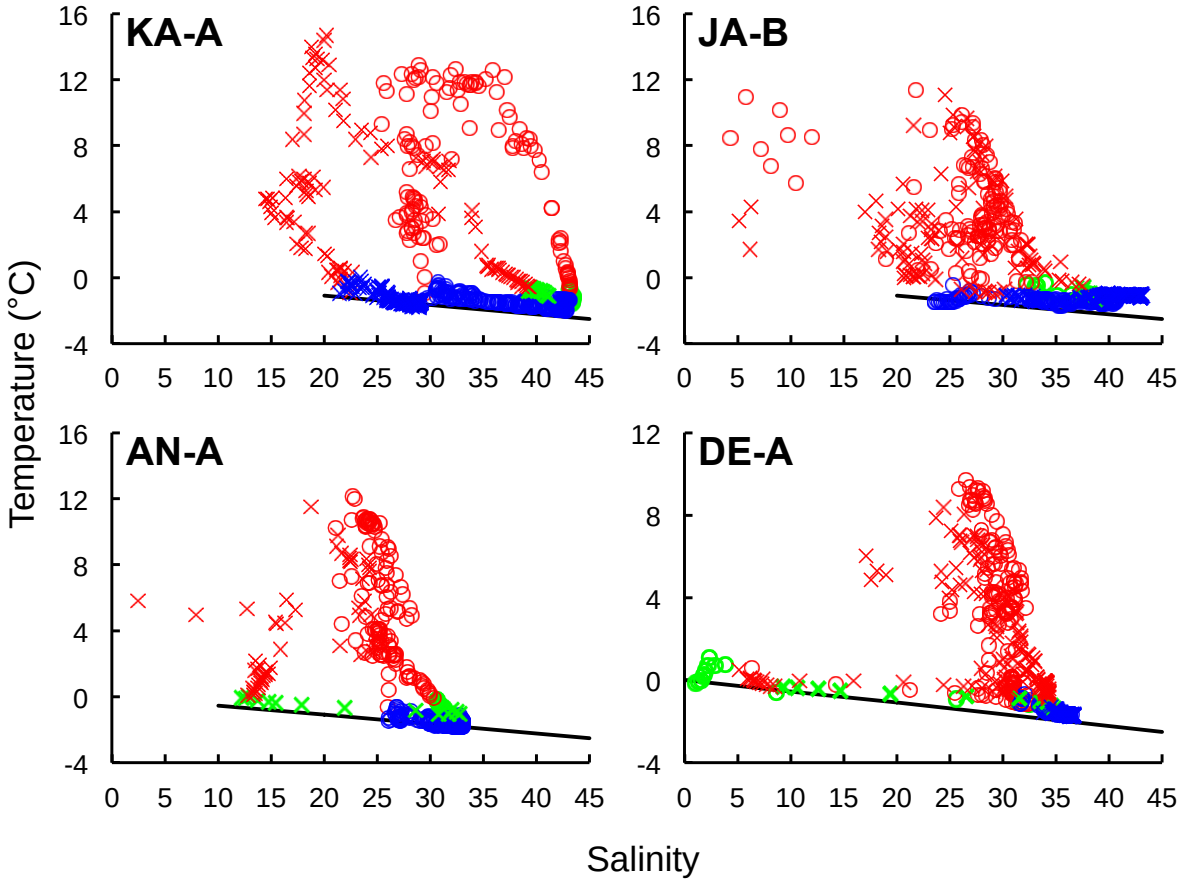

Figure 1.5 Temperature-Salinity (T-S) scatterplots show daily average values from HOBO loggers located furthest from lagoon channels in each lagoon.
The solid line is the freezing point curve as a function of salinity. Symbols denote the year (o = winter 2011/12, spring and summer 2012, x = winter 2012/2013, spring and summer 2013), colors denote the season (red = summer open-water period, green = spring break-up period, and blue = winter ice-cover period). Spring breakup is defined as the first two weeks in June.

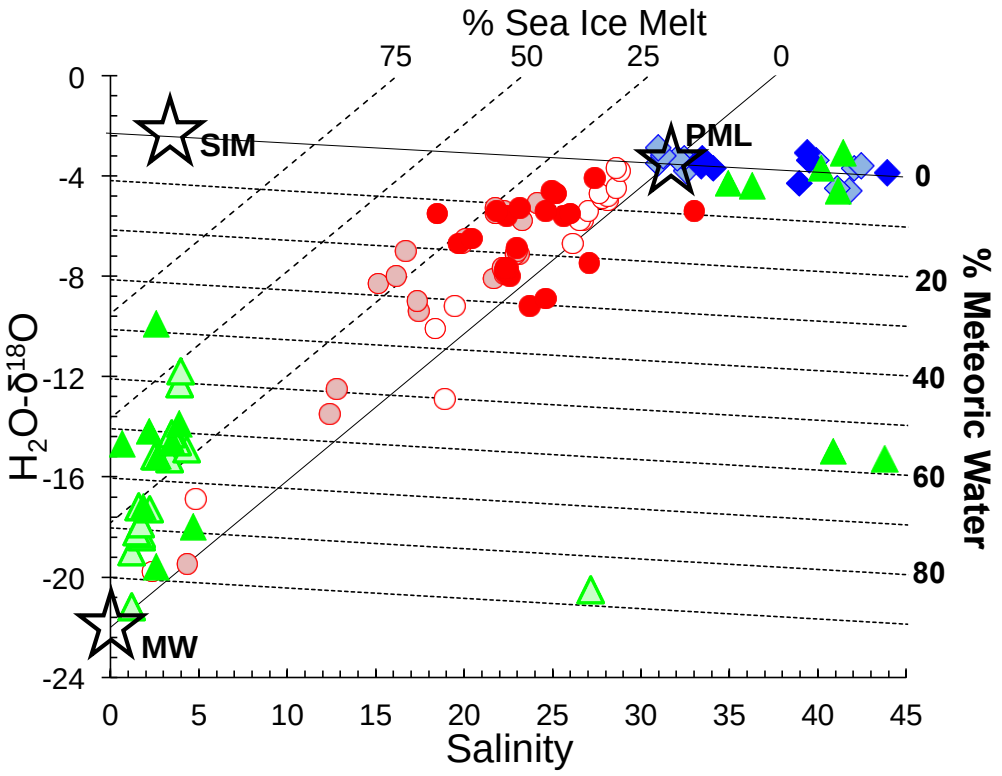

Figure 1.6A Relationship between H_2O - $\delta^{18}O$ and salinity.
Water samples were collected from 1 m (open symbols), 2 m (shaded symbols), or ≥ 3 m (filled symbols) at each lagoon during the three sampling months (blue diamonds = April, green triangles = June, red circles = August) from all sampling years. The solid line shows the expected mixing line between PML and MW (see methods for more details). Dashed lines show the estimated fractions of low salinity water derived from sea ice melt and meteoric water (bolded). Water sources are shown as hollow stars (SIM = sea ice melt, MW = meteoric water, PML = Polar Mixed Layer).

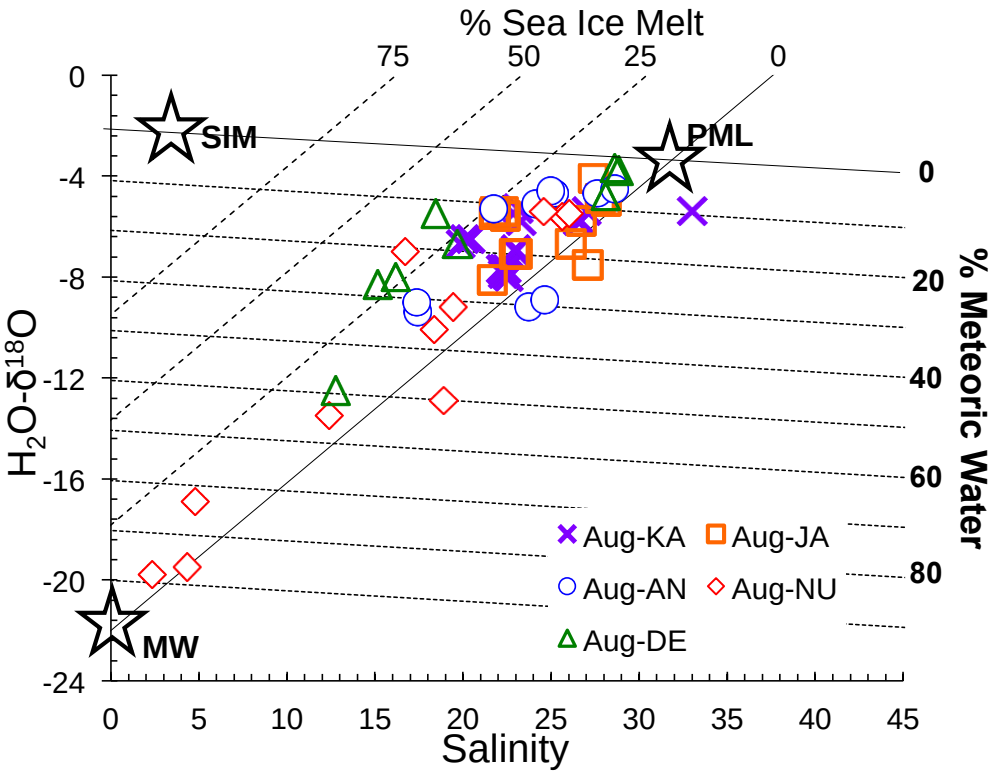

Figure 1.6B Relationship between H_2O - $\delta^{18}O$ and salinity for samples collected in August from all lagoons. Samples from all depths are shown.
Dashed lines show the estimated fractions of low salinity water derived from sea ice melt and meteoric water (bolded). Water sources are shown as hollow stars (SIM = sea ice melt, MW = meteoric water, PML = Polar Mixed Layer).

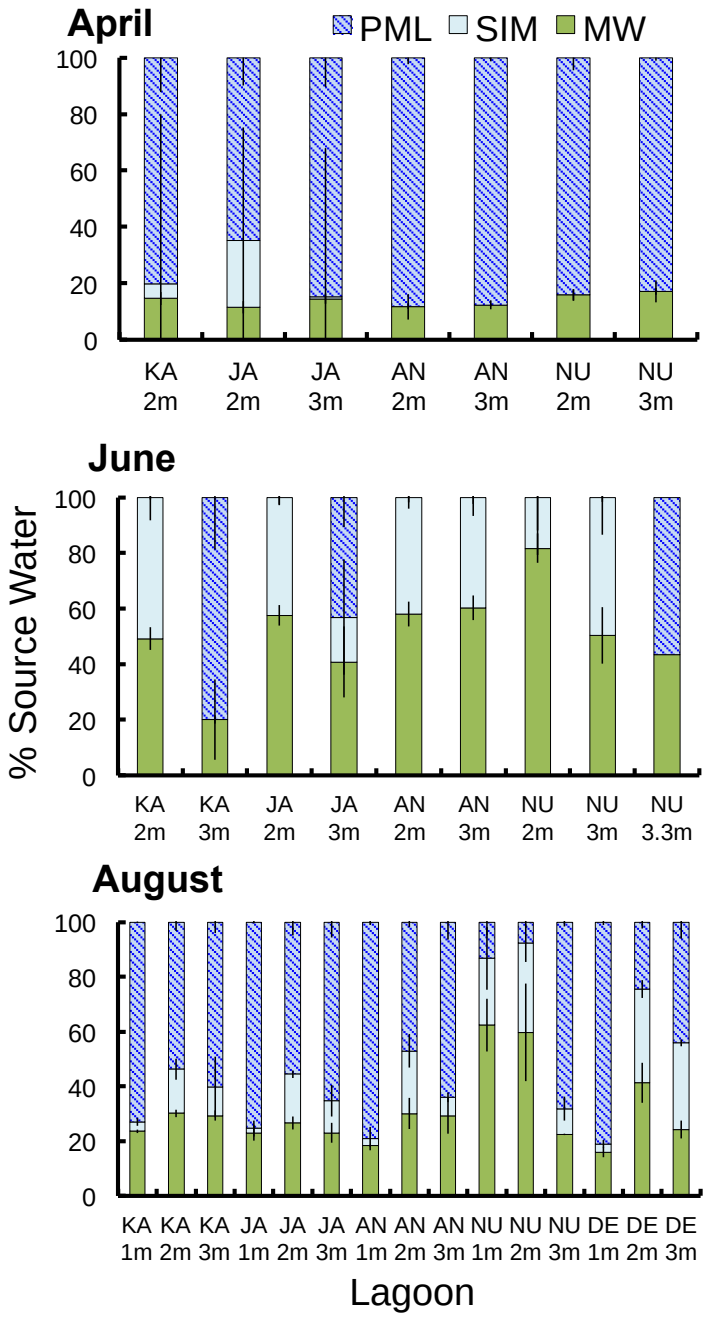

Figure 1.7 The modeled % of source waters (Polar Mixed Layer (PML), sea ice melt (SIM), and meteoric origin (MW)) present in lagoons at different depths during the three sampling seasons.
Data from all stations and all sampling years are averaged. Error bars show SE. If model results were above 100% or below 0% for a source, that value has been rounded to 100 or 0, respectively.

Chapter 2. Importance of terrestrial carbon subsidies to nearshore eastern Alaskan Beaufort Sea food webs

ABSTRACT

Lagoons are a prominent feature of Arctic coastlines, support diverse benthic food webs, and provide vital feeding grounds for fish, migratory birds, and mammals. In these lagoons, terrestrial organic carbon (C_T) from watershed runoff and coastal erosion, which are predicted to increase under global warming, may subsidize marine organic carbon (C_M) as an energy source for consumers. Because C_T is ^{13}C depleted relative to marine phytoplankton and benthic microalgae, we used a stable isotope mixing model (IsoError) to determine the proportion of C_T and C_M assimilated by resident fauna, including animals widely used by local subsistence hunters. In addition, stable nitrogen isotope values were used to assess consumer trophic levels. Isotopic composition was determined for 39 faunal taxa collected along the eastern Alaskan Beaufort Sea coast as well as end-member carbon sources. Mean $\delta^{13}C$ values for animals ranged from -25.0‰ (*Monoporeia affins,* amphipod) to -17.1‰ (*Weyprechtia* spp*.,* amphipod), implying that consumers assimilate variable amounts of marine and terrestrial carbon sources. Mean $\delta^{15}N$ values for animals ranged from 7.2‰ (*Molgula spp.,* sea squirt) to 20.3‰ (*Ursus maritimus,* polar bear), revealing that Beaufort Sea coastal ecosystems can support up to five trophic levels. The mixing model suggests that upper trophic level consumers assimilate substantial amounts of C_T along with marine-derived C sources. For example, 15 - 70% of polar bear (trophic level 4.9) carbon and 0 - 60% of beluga whale (TL 4.3) carbon was of terrestrial origin. Our results suggest that 1) C_T assimilated by benthic omnivorous invertebrates is transferred to the highest trophic levels in the Beaufort Sea, and 2) Arctic cod are the most likely intermediary for transferring C_T from lower to upper trophic levels.

INTRODUCTION

Arctic coastal systems are sensitive to global climate change as a result of changing land-sea interactions (McClelland et al. 2012). Water discharge from the major Arctic rivers has increased with warming temperatures (Peterson et al. 2006), although the changes have not been uniform across the pan-Arctic domain (McClelland et al. 2006), and decreases are anticipated in some areas. For example, glacial runoff from the Brooks Range to the eastern Alaskan Beaufort Sea is predicted to decrease as glaciers shrink, possibly disappearing completely in the next 50 years (Nolan et al. 2011). Enhanced storm activity coupled with greater permafrost thaw and loss of shore-fast sea ice has also increased coastal erosion rates over the past 15 years (Lantuit et al. 2012, Barnhart et al. 2014). In order to accurately predict the impact of these types of changes on coastal Arctic ecosystems, we must first characterize contemporary ecosystem conditions. It may be too late to evaluate truly "baseline" conditions because recent research shows that Arctic coastal ecosystems are already responding to anthropogenic environmental changes (e.g., Wassmann et al. 2011), but the current study can be used as a reference against which to compare subsequent work.

Lagoons, bounded by barrier islands to the north and Alaska's Arctic slope to the south, span over 50% of the Alaskan Beaufort Sea coastline. These lagoons link marine and terrestrial ecosystems and support productive biological communities that provide valuable habitat and feeding grounds for many ecologically and culturally important species. Beaufort Sea lagoons are ice-bound for approximately nine months out of the year; therefore, the brief summer open-water period is an especially important time for resident animals to build energy reserves (necessary for spawning and surviving for the

winter months) and for migratory animals to feed in preparation for fall migrations (Brown et al. 2012).

Several studies have examined the benthic community structure of lagoons along the eastern Alaskan Beaufort Sea. Faunal communities in the lagoons include bivalves, gastropods, polychaetes, ascidians, sponges and crustaceans (Dunton et al. 2012), and are dominated by opportunistic omnivores and detritivores (Craig 1984). Epibenthic organisms, in particular polychaetes, mysids, and amphipods, are important prey items for larger consumers such as fish and birds during the open water period. Over 150 species of migratory birds from six continents, including waterfowl (Brown 2006), and marine and anadromous fish (von Biela et al. 2011), rely on Arctic lagoons and nearby river deltas for summer habitat and feeding grounds. Dominant fish species include Arctic cod (*Boreogadus saida*), Arctic flounder (*Plueronectes glacialis*), Arctic char (*Salvelinus alpinus*), and several sculpin species (*Myoxocephalus* spp.) (Craig et al. 1982).

Some lagoon species, such as mysids, amphipods, and fishes, seasonally migrate or are advected to adjacent nearshore areas outside the barrier islands and contribute to the diets of fish (as well as marine mammals) living within the shelf domain (Dunton et al. 2006, Fechhelm et al. 2009). Seals, toothed whales, and polar bears (*Ursus maritimus*), as well as local subsistence hunters, consume these fishes (Kruse 1991). Arctic cod, in particular, are thought to be a key link that transfers energy from primary consumers to upper trophic levels (Craig et al. 1982; Bradstreet & Cross 1982). Mature Arctic cod feed mainly on amphipods and mysids, though zooplankton are a substantial food source for juveniles (Craig et al. 1982; Walkusz et al. 2011; Dunton et al. 2012). Beluga (*Delphinapterus leucas*) and bowhead whales (*Balaena mysticetus*), which are

also important to the subsistence and cultural heritage of the Beaufort Coast, forage in the open water outside of lagoons during summer months (Pedersen and Linn 2005).

Because light limitation results in a very short growing period, it has been hypothesized that Arctic nearshore ecosystems rely on terrestrial organic matter (C_T) inputs to sustain their characteristically productive and diverse food webs (Dunton et al. 2006, 2012, McClelland et al. 2012, 2014). C_T input rates depend on the quantity of freshwater discharge from Arctic rivers and on the concentrations of organic matter (OM) in those rivers (McClelland et al. 2012), as well as erosion rates of the bordering coastline. In the Alaskan Beaufort Sea, coastal erosion and fluvial transport combined annually deliver an amount of OM roughly equal to all the marine primary production within 10 km of the coast (Schell 1983a), which highlights the importance of C_T in the Beaufort region.

Stable isotope analysis (SIA) is routinely used to examine trophic structure and carbon assimilation pathways, and has been successfully applied to the Arctic marine environment (Hobson et al. 1995, Iken et al. 2005, von Biela et al. 2011, Dunton et al. 2012, Connelly et al. 2014). Carbon (C) SIA is one method of assessing the relative contribution of marine and terrestrial OM to an organism's diet, because these sources have different $\delta^{13}C$ values (Hobson et al. 1995). Typically, $\delta^{13}C$ values of tundra plants range from -30 to -25‰, marine phytoplankton range from -25 to -18‰, and marine benthic microalgae (diatoms) range from -13 to -20‰ (Parsons et al. 1989; Dunton & Schell 1987; Schell et al. 1989; Dunton et al. 2012). SIA provides a longer-term estimate (weeks to months) of diet than gut content analysis. It also provides information on what food sources are assimilated after ingestion. Nitrogen (N) SIA is useful for examining trophic structure because they exhibit ~2 to 4‰ (mean 3.4‰) enrichment between trophic levels (Post 2002).

Studies have applied natural abundance stable C isotope analysis techniques to Beaufort Sea ecosystems and found increasingly depleted $\delta^{13}C$ values with decreasing longitude (west to east along the coast) in sediments (-21 to -27‰; Dunton et al. 2012), copepods (-20.9 to -26.7‰; Saupe et al. 1989), benthic invertebrates (-19 to -26‰ for suspension feeders, Dunton et al. 1989), and bowhead whales (-18.8 to -20.7‰ in muscle tissue, Schell et al. 1989). Depleted $\delta^{13}C$ values may imply greater reliance on terrestrially-derived carbon, reflecting major inputs from the Mackenzie River in Canada as well as inputs from numerous smaller rivers along the eastern Alaskan Beaufort Sea coast (Dunton et al. 2006, Iken et al. 2010).

Several studies that have examined food web dynamics in the coastal Beaufort Sea, focused primarily on benthic invertebrates, and found that lagoon benthos provide a concentrated area of preferred prey items to upper trophic consumers (Craig et al. 1982; Dunton et al. 2006; Dunton et al. 2012). Because previous work has demonstrated that benthic invertebrates assimilate C_T during the open water period, it follows that C_T may be important to apex consumers like adult fish, seals, polar bears, and toothed whales. This transfer of terrestrial OM to upper trophic levels is inferred, but has not been quantitatively explored.

This study examines terrestrial subsidies to faunal communities in estuarine lagoons and nearshore waters of the eastern Alaskan Beaufort Sea. We apply stable nitrogen and carbon isotopic analysis to *1)* determine trophic relationships among lagoon and nearshore biota and *2)* quantify the importance of terrestrially-derived carbon to lagoon and nearshore biota using representative C_T and marine carbon (C_M) isotope end-members. Particular attention is paid to upper level consumer species that are important subsistence and cultural species on the North Slope. These species include adult fish [Char (*Salvelinus* spp.), and Cisco (*Coregonus* spp.)] as well as the yellow-billed loon

(*Gavia adamsii*), beluga whale (*Delphinapterus leucas*), and polar bear (*Ursus maritimus*). We hypothesize that animals will occupy similar trophic positions in lagoons and the nearshore environment, but that animals in lagoons will assimilate more terrestrially-derived carbon than congeners in adjacent nearshore waters.

METHODS

Study area

Our study area included four lagoon sites, three sites in adjacent shelf waters (*nearshore*), four offshore sites (*marine),* and two river sites in the eastern Alaskan Beaufort Sea coast, near Barter Island (**Fig. 2.1).** Kaktovik Lagoon (KA) is almost fully enclosed and only receives freshwater inputs from small tundra streams and runoff (Dunton et al. 2012). Jago Lagoon (JA), a largely open lagoon east of KA, is separated from KA by a peninsula and receives direct freshwater inputs from the Jago River. Angun (AN) and Nuvagapak (NU) Lagoons, located further east, are semi-enclosed, and receive inputs form smaller rivers. The Jago River empties into JA and the Hulahula River empties into Camden Bay, located 10 km west of Kaktovik lagoon.

The Beaufort Sea coast experiences weak lunar tides (mean 10 cm) (NOAA 2010). Exchange between lagoons and the nearshore environment occurs via shallow channels between barrier islands. The lagoons are estuarine during the ice-free months of the summer (July to early-September), and their salinity regimes vary based on rate and magnitude of freshwater inputs. On average during the summer, lagoon waters are warm (11 ± 2 °C (mean ± SD)) and brackish (21 ± 7) (Connelly et al. 2015). Overall, the Beaufort Sea coast is strongly influenced by river runoff. The Mackenzie River, which is the largest river emptying into the North American Arctic, is 400 km east of Barter Island

and discharges 380 km^3 of freshwater annually (Macdonald et al. 2004). Smaller rivers that flow directly into the lagoons also greatly influence the physical and chemical environment, especially during the spring freshet period (McClelland et al. 2006, 2014).

Sample collection and analysis

Food web components, including suspended particulate organic matter (SPOM), benthic particulate organic matter (BPOM), and fauna were collected from lagoon, nearshore, and marine sites during August 2011 - 2014 aboard the *R/V Proteus* and aboard the *R/V Norseman II* (**Table 2.1**). Samples were collected from two to three stations within each lagoon, all of which were 2 - 4 m deep, and at each nearshore station, which ranged in depth from 4 to 10 m, on 7 - 18 August 2011, 7 - 15 August 2012, and 10 - 13 August 2013. The four marine sites, located 20 km offshore at 35 - 37 m water depth, were sampled once for SPOM and BPOM on 2 August 2014.

Two North Slope river sites were also sampled. SPOM was collected from the Jago River six times between 6 and 23 August 2012, and from the Hulahula River three times between 13 and 17 August 2011. Several juvenile Arctic char (*Salvelinus alpinus*) were collected from the Hulahula River as well (on 13 August 2011).

At each lagoon and nearshore station, a YSI 600 XLM data sonde was used to record temperature and salinity from several depths throughout the water column. We collected fauna using an Ekman grab and 1 m beam trawl. Water samples were collected using 4 L carboys submerged to approximately ~0.5 m depth. Within hours of collection water samples were filtered in duplicate for particulate organic matter (SPOM) concentration and stable carbon and nitrogen isotope analysis onto pre-ashed 25 or 47 mm Whatman GF/F filters and dried at 60 °C in petri dishes.

Two or three Ekman grabs (0.023 m^2) per station (lagoon and nearshore only) were used to sample infaunal organisms and sediment. BPOM samples were collected from each Ekman sample in duplicate using 20 cm^3 syringe cores (1.8 cm diameter, 1 cm depth). BPOM samples were dried at 60°C in plastic snap-cap vials prior to preparation for stable isotope analysis. The remaining sediment in the grabs was sieved (1 mm) for benthic invertebrate collection.

At marine stations only, a 20 μm plankton net was used to collect phytoplankton. The net was deployed vertically to 2 m above the sea floor. The contents retained in the cod end were sieved through a 63 μm sieve. The 20-63 μm size fraction was collected and filtered in duplicate onto a pre-ashed 25 mm Whatman GF/F filters, which were dried at 60 °C in aluminum dishes in preparation for stable isotope analysis.

A 1 m beam trawl (1 mm mesh size) was towed for ~10 minutes at each lagoon and nearshore station to collect epibenthic organisms. Trawl contents were collected on a 1 mm sieve, sorted into separate vials, and stored at 5 °C for later identification. All animals were handled in accordance to IACUC permit #AUP-2012-00103. Within one day of collection, all organisms (invertebrates and some small (< 10 cm) fish) were rinsed in filtered seawater at the field station and identified to the lowest taxonomic unit possible, usually species. All animals were sampled in triplicate when possible, and dried to a constant weight at 60 °C in aluminum dishes. Small animals were dried whole (e.g., polychaetes, priapulids, and small crustaceans); muscle tissue was isolated from large organisms (bivalves, gastropods, large crustaceans, and fish) prior to drying. When taxa were small, multiple individuals of the same species were pooled to collect sufficient biomass for isotope analysis.

All large animal samples (birds, mammals, and fish > 10 cm) were acquired during mid-July through mid-September in 2012, 2013, 2014, and 2015. Most samples

were graciously donated by local Inupiat hunters and fishers or contributed by U.S. Fish and Wildlife Service biologists working with the Arctic National Wildlife Refuge. We distributed sample bags to local hunters at the start of the open-water period and most samples were received in these bags, labeled with the date, approximate location and method of capture, and common name of the sample that was acquired. Muscle tissue was isolated from all large animal samples prior to drying to a constant weight at 60 °C in plastic snap-cap vials.

Over 1,200 organisms were collected, from which 200 organisms from seven phyla and twenty-seven orders were analyzed. Dried samples were transported to the University of Texas Marine Science Institute (UTMSI) in Port Aransas, TX for stable isotope preparation and analysis.

Isotope analysis

All SPOM, BPOM, and fauna samples were analyzed for stable C and N isotope values. First, dried fauna and BPOM samples were homogenized with a mortar and pestle. Two homogenized subsamples were analyzed for BPOM samples, SPOM filters, phytoplankton filters, calcifying animals, and animals from which muscle tissue was not isolated. One subsample was treated with acid to remove carbonates by soaking in 1 N HCl until bubbling ceased, rinsed twice in de-ionized (DI) water, re-dried at 60 °C, and analyzed for C isotope analysis. A separate, non-acidified sample was analyzed for N isotope analysis. All animal samples that did not require acidification were analyzed once for dual C and N isotope analysis. Preparation and analyses of SPOM samples are detailed in Connelly et al. 2015.

Dried samples were weighed into tin capsules and analyzed for C and N content and isotopic composition on a Finnigan MAT Delta Plus continuous flow isotope ratio

mass spectrometer (CF-IRMS) coupled to a Carlo Erba 1500 elemental analyzer (EA) at UTMSI. Isotope values are expressed in delta (δ) notation:

Eq. 1: $\delta^{13}C$ (or $\delta^{15}N$) (‰) = [(R_{sample} / $R_{standard}$) − 1] x 1000

Where R is $^{13}C/^{12}C$ (or $^{15}N/^{14}N$) and the standard reference is Vienna Pee Dee Belemnite or atmospheric nitrogen (N_2), respectively. Based on internal standards, which were run every 12th sample, instrumental analytical error was ± 0.2**‰.** If acidified and non-acidified subsamples were analyzed, molar C:N ratios for those samples were calculated using the carbon and nitrogen content in micromoles from the acidified subsample only.

Although the process of assimilating carbon into an animal's tissues may take several weeks to several months (~ 20 days for an Arctic amphipod; Kaufman et al., 2008, four weeks for an Arctic bivalve; McMahon et al., 2006), our samples were all collected from late-July to early-September. Therefore, we are confident that the isotopic composition of whole-body and muscle tissue of most of the animals sampled in this study reflect their diet post-ice break up (which typically occurs in mid June).

Lipid bias

Lipids are known to be inherently depleted in ^{13}C relative to other tissues, such as proteins and carbohydrates (DeNiro and Epstein 1977), and may be a confounding variable in food web studies that utilize stable carbon isotopes. Post et al. 2007 found a positive correlation between lipid content (as indicated by C:N ratio) and $\delta^{13}C$ value of whole organisms if tissues had C:N > 3.5, and suggested researchers apply mathematical equations to remove lipid bias from bulk tissue $\delta^{13}C$ values. Some polar studies, however, have found no relationship between bulk $\delta^{13}C$ and C:N ratio (Dunton 2001, Dunton et al. 2012).

A recent study by Smith et al. (in review) examined the $\delta^{13}C$ of the lipid fraction of the *Calanus* copepods, *Onisimus* amphipods, and mysids (*Mysis*) collected in this study. Smith et al. found that the $\delta^{13}C$ values of bulk lipids varied by ~6‰ among the crustaceans examined, which questions the utility of a one-size-fits-all mathematical equation to "correct" for lipid content; consequently, adjustment of the original isotopic value may introduce more bias than it removes.

The present study found no significant relationship between bulk $\delta^{13}C$ values and C:N of lagoon and nearshore genera (**Fig. 2.2**). Based on this lack of correlation and the results of Smith et al. (in review), no post-analysis adjustments of the data were applied to account for "lipid bias." Because lipids are important energy reserves for Arctic animals (Møller and Hellgren 2006), and the process of lipid extraction may also compromise other tissue constituents, no lipid extractions were performed on our samples to avoid the potential loss of critical information and introduction of error into the food web analysis.

Trophic guild assignment

Invertebrate species were classified as suspension/ filter feeders, deposit feeders, or epibenthic omnivore based on taxonomic data from Macdonald et al. (2010), and the World Register of Marine Species (Appeltans et al. 2012). Data for the genus was used if species-specific data was unavailable.

Trophic level determination

Stable N isotope values were used to estimate each taxon's trophic level within the lagoon-nearshore food web (Fry 2006). As is common in Arctic studies, *C. hyperboreus*, a calanoid copepod, was used as a TL baseline because it is a known herbivore and is thus assumed to occupy TL 2 (Hobson and Welch 1992, Hobson et al.

2002, Hoekstra et al. 2002). The mean lagoon *C. hyperboreus* $\delta^{15}N$ value across all years was 11.0‰ and the mean nearshore *C. hyperboreus* $\delta^{15}N$ value was 10.5‰. These values were used to calculate TLs for the lagoon and nearshore biota, respectively. The trophic level (TL) of all individuals was calculated using the $\delta^{15}N$ enrichment relative to *Calanus hyperboreus* $\delta^{15}N$ (TL = 2) and a trophic enrichment factor of 3.4‰.

Eq. 2: $$TL = [(\delta^{15}N_{consumer} - \delta^{15}N_{C.\ hyperboreus}) / 3.4] + 2$$

Although trophic enrichment factors between consumers and food sources vary, 3.4‰ is used here because Post (2002) reported this as the average for aquatic consumers and this factor has successfully been applied to other Arctic food web studies (e.g. Iken et al. 2010; Dunton et al. 2012; McTigue & Dunton 2014). Because *C. hyperboreus* is not present in rivers, the mean river SPOM $\delta^{15}N$ value across all years (2.9‰) was used as the baseline for river fish TL determination. As SPOM represents a primary food source (TL 1), 1 instead of 2, was added as the final step in Equation 2.

Quantifying terrestrial subsidies

$\delta^{13}C$ analysis was used to estimate assimilation of C_T and C_M by consumers. We first assessed animal reliance on C_T and C_M by constructing isotope biplots that depict the full range of potential trophic enrichment factors. In the biplots, enrichment lines extend from the three carbon sources (terrestrial, phytoplankton and benthic microalgae/ microphytobenthos (MPB)) show the expected isotope values of consumers feeding exclusively on each carbon source. The pair of lines emanating from each carbon source represents the maximum and minimum reported increase in $\delta^{13}C$ (0.8 and 2‰) and $\delta^{15}N$ (3 and 4‰) with increasing trophic level (Post 2002, Fry 2006), thereby accounting for variation in trophic enrichment factors which can impact the estimation of reliance on C_T.

This graphic depiction constitutes a visual method of determining the reliance of consumers on basal carbon sources.

IsoError, a two-source isotope mixing model developed by Phillips and Gregg (2001), was used to quantify the percent of terrestrial and marine carbon present in biota samples by converting stable C isotope signatures to % diet contribution data. IsoError calculates the proportions (and standard errors) of the contributions that two end-members make to a mixture (biota sample). This model is unique because it accounts for isotope variance in the end-members and the resulting mixture (Phillips and Gregg 2001). This analysis was conducted at the genus level, If n=1 for a particular genera, SD was assumed to be 1‰.

To account for trophic enrichment of carbon isotopes, we applied a correction factor to biota isotope values used in the IsoError model (Eq. 3 below is a simplified example of the IsoError equations). The trophic enrichment correction factor, *E*, was calculated by multiplying 1‰ (the average reported increase in $\delta^{13}C$ with trophic level (Post 2002)) by the derived trophic level for each genera. Variation in this trophic enrichment factor is not accounted for in the IsoError model. In Eq. 3, $\%C_T$ is the percent of carbon derived from terrestrial sources and $\delta^{13}C_M$ and $\delta^{13}C_T$ are representative end-members.

$$\text{Eq. 3: } \%C_T = [(\delta^{13}C_{biota} - \delta^{13}C_M) - E / (\delta^{13}C_T - \delta^{13}C_M)] * 100$$

Because there are two main types of marine carbon in the nearshore Beaufort Sea, phytoplankton and benthic microalgae (microphytobenthos), we ran the IsoError model twice, once using the marine phytoplankton signal (-24.6 ± 0.9‰; this study) as $\delta^{13}C_M$ and once using the MPB signal (-17.5 ± 1.5‰; literature value) as $\delta^{13}C_M$. It is likely that organisms consume a mixture of phytoplankton and MPB, so this method allows us to assess the minimum (using phytoplankton $\delta^{13}C$, which is less enriched) and maximum

(using MPB $\delta^{13}C$, which is more enriched) percent of a consumer's tissue that was supported by C_T.

To accommodate the range in end-member values reported in the literature and observed in this study, a mean and standard deviation were entered for each end-member. The $\delta^{13}C_T$ value used is -29.0 ± 0.7‰ (mean river SPOM reported here). This range encompasses the most depleted estuarine SPOM value observed in the present study (-28.9‰ in lagoons in 2012) and the tundra peat values reported by Schell (1983), and falls within the extremes observed for North Slope river SPOM by McClelland et al. (2014).

We used a $\delta^{13}C_{phytoplankton}$ value of -24.6 ± 0.9‰ based on our average 20 μm plankton net samples from marine sites. This value agrees well with the mid-water column SPOM value from the Beaufort Sea shelf (-24.8‰) reported in Dunton et al. (2012). The $\delta^{13}C_{MPB}$ value used is -17.5 ± 1.5‰, which represents a mean of benthic diatom isotope values reported in the literature (France 1995; Newell et al. 1995; Cloern et al. 2002; Kang et al. 2003), as well as ice algae values from the Chukchi Sea (-18.9 ± 0.8‰, Dunton, unpublished data). If $\delta^{13}C_{biota}$ is less than $\delta^{13}C_T$ or greater than $\delta^{13}C_M$, the IsoError model provides unrealistic values of $\%C_T$ and $\%C_M$. In these cases, we assume the biota is 100% reliant on the end-member with the most similar $\delta^{13}C$ signal.

Although the IsoError model accounts for variation in end-member and biota isotope values, it does not account for variation in trophic enrichment factor. Inspection of biplots provides a visual method of assessing C_T reliance that incorporates variation in trophic enrichment factors, though it does not quantify the reliance of each genus on C_T. Therefore, combining the IsoError model with the biplot approach provides a more robust indication of the importance of terrestrial carbon to upper level consumers.

Statistical analysis

All statistical tests were performed in GraphPad PRISM statistical software (Version 6, 2013). Significance was assessed using $\alpha = 0.05$.

Sources of organic matter

A one-way ANOVA with Tukey's multiple comparison post-hoc test was used to determine differences in BPOM $\delta^{13}C$, because the residuals were normally distributed as assessed by a Shapiro-Wilk normality test and Bartlett's test for homogeneity of variance ($p < 0.05$). Non-parametric Kruskal-Wallis tests with Dunn's multiple comparison post-hoc test were used to determine differences in SPOM $\delta^{13}C$ and $\delta^{15}N$ values among all four site types and among BPOM $\delta^{15}N$ values from three site types (lagoon, nearshore, and marine), because the data did not meet the assumptions of homoscedasticity.

Mann-Whitney rank tests were used to test for differences in $\delta^{13}C$ and $\delta^{15}N$ values between SPOM and BPOM samples at each site type (lagoon, nearshore, and marine). A non-parametric test was used because residuals were not normally distributed as assessed with a Shapiro-Wilk normality test.

To avoid overrepresentation of a single site, data from each station within a site were averaged to generate one SPOM value and one BPOM value per site per sampling year.

Site type comparisons of biota

Unpaired, two-tailed t-tests were used to test for differences in $\delta^{13}C$ and $\delta^{15}N$ values between the same taxa collected from two site types if $n \geq 2$ for each taxa. Analyses were conducted at the genus level. Specifically, we tested whether C or N isotopes for *Portlandia*, *Mysis*, *Calanus*, *Boreogadaus, Priapulus* and *Myoxocephalus*

differed between lagoon and nearshore stations. We also tested whether C or N isotopes for *Salvelinus* differed between lagoon and river stations.

RESULTS

Sources of organic matter

SPOM data from lagoon and nearshore sites was originally published by Connelly et al. (2015). $\delta^{13}C$ and $\delta^{15}N$ values differed depending on site type for SPOM ($\delta^{13}C$: K-W stat = 14.57, $p = 0.002$; $\delta^{15}N$: K-W stat =12.26, $p = 0.007$) and for BPOM ($\delta^{13}C$: $F_{(2,18)} = 9.06$, $p = 0.002$; $\delta^{15}N$: K-W stat = 10.51, $p = 0.006$) (**Table 2.2, Fig. 2.3**). River samples had the most depleted SPOM $\delta^{13}C$ and $\delta^{15}N$ (-29.0 and 3.3‰ respectively), and marine samples had the most enriched SPOM $\delta^{13}C$ and $\delta^{15}N$ (-21.9 and 8.9‰ respectively). Post-hoc tests confirmed that these differences were significant. A gradient from depleted to enriched C and N isotope values from river to lagoon to nearshore to marine sites was observed (**Fig. 2.3**). Lagoon SPOM (-27.2‰) was more ^{13}C depleted than marine SPOM; nearshore SPOM (-26.0‰) did not differ from any other site type. Nearshore SPOM (7.1‰) was more ^{15}N enriched than river SPOM; lagoon SPOM (6.3‰) did not differ from any other site type. Lagoon BPOM (-27.3‰) was more ^{13}C depleted than marine and nearshore BPOM (-26.0‰) and both nearshore (2.8‰) and lagoon BPOM (3.2‰) were more ^{15}N depleted than marine BPOM. River BPOM was not collected. SPOM was significantly more enriched in ^{15}N than BPOM at lagoon, nearshore, and marine sites (**Table 2.3**). SPOM was only significantly more enriched in ^{13}C relative to BPOM at marine sites.

Consumer isotope values

Both $\delta^{13}C$ and $\delta^{15}N$ varied greatly among the biota sampled from lagoon and nearshore stations. The $\delta^{13}C$ values of consumers spanned from -25.0‰ to -17.1‰ (**Table 2.4, Fig. 2.4A**), while the $\delta^{15}N$ of consumers ranged from 7.2‰ to 20.3‰ (**Fig. 2.4B**).

Trophic levels

Trophic level calculations revealed that coastal systems along the eastern Alaskan Beaufort Sea support up to five trophic levels (**Tables 2.4, 2.5**). Some organisms occupy a TL < 2, which likely implies they are primary consumers that either feed on food sources more depleted in ^{15}N than the diet of *Calanus* and/ or that their enrichment relative to their food source is less than the factor (3.4‰) we employed. In lagoons, TL 2 was comprised mostly of amphipods, bivalves, and polychaetes, most of which are deposit-feeders, as well as a filter-feeding bryozoan (*Eucratea loricata*), a filter-feeding ascidian (*Molgula griffithsii*), and the calanoid copepod *Calanus hyperboreus*. TL 3 contained twenty genera, mostly epibenthic omnivores, including *Nereimyra aphroditoides* polychaetes, mysids, *Atylus carinatus* and *Onisimus glacialis* amphipods, and *Portlandia Arctica* bivales and *Cylichna alba* gastropods. Arctic cod (*Boreogadus saida*), slender eelblenny (*Lumpenus fabricii*), and Arctic flounder (*Plueronectes glacialis*), are all small epibenthic predators were also in TL 3. TL 4 contained four genera of larger, predatory fish.

The coastal environment is also home to many larger animals. Of these species, the common eider (*Somateria mollissima*) and white-fronted goose (*Anser albifrons*) occupied TL < 2, which implies our equation may not be appropriate for these species that likely rely on an unsampled non-riverine plant source. The predatory loon (*Gavia adamsii*) occupied TL 3.6. For marine mammals, the bowhead whale (*Balaena mysticus*)

occupied TL 2.7 and the top predators of this system were bearded seal *Erignathus barbatus* (TL 4.0), beluga whale *Delphinapterus leucas* (TL 4.3), and polar bear *Ursus maritimus* (TL 4.9).

Site Type comparison

Overall, animals from nearshore stations were isotopically similar to congeners collected from lagoons, though not all species displayed this trend (**Fig. 4**). Six out of eleven genera collected from both lagoon and nearshore sites had sufficient sample size to facilitate a statistical comparison (see Methods section 2.4 for more details). Four genera showed no significant C isotopic differences and five genera showed no significant N isotopic differences. *Portlandia arctica* were more enriched in ^{13}C ($t_{(5)}$ = 2.7, p = 0.045) at nearshore stations. Sculpin (*Myoxocephalus* spp.) from lagoons were more enriched in both ^{13}C ($t_{(12)}$ = 5.0, $p < 0.0003$) and ^{15}N ($t_{(12)}$ = 2.9, p = 0.013) than at nearshore stations. This difference in sculpin ^{15}N values translated into a substantial difference in trophic level between lagoon (TL 3.1) and nearshore (TL 2.6) sites. *Salvelinus* spp. were more depleted in ^{13}C ($t_{(7)}$ = 2.6, p = 0.035) and ^{15}N ($t_{(7)}$ = 6.6, $p <$ 0.0003) at river stations than at lagoon stations.

Assessing terrestrial subsidies

The IsoError mixing model and biplot enrichment line approach yielded similar results. Taxa for which the IsoError model indicated > 10% of carbon originated from terrestrial sources tended to plot between the C_T and C_M enrichment lines on biplot graphs (**Fig. 2.5)**.

Most deposit feeding invertebrates, with the exception of the amphipod *Monoporeia affins* from lagoons and the penis worm *Priapulus caudatus* from the nearshore environment, appear to rely mostly on marine carbon sources (**Fig. 2.5A**). All

suspension feeding and grazing invertebrates likely consume material derived from terrestrial and phytoplankton sources, with the exception of the nearshore bryozoan *Eucratea loricata*, which plots within the C_T enrichment lines (**Fig. 2.5B**). Although the majority of epibenthic omnivorous fauna cluster between the $C_{phytoplankton}$ and C_{MPB} marine enrichment lines, two lagoon fishes and two nearshore fishes are more depleted in ^{13}C than the $C_{phytoplankton}$ enrichment line with the steepest slope (**Fig. 2.5C**). Omnivorous fishes appear to consume more terrestrially-derived material than omnivorous invertebrates. River fish plot close to the terrestrial enrichment line with the steepest slope. All birds plotted between the $C_{phytoplankton}$ and C_{MPB} enrichment lines (**Fig. 2.5D**). Bearded seal (*Erignathus barbatus*) and bowhead whale plot between the $C_{phytoplankton}$ and beluga and bowhead whale both plot between C_T and $C_{phytoplankton}$ and C_{MPB} lines. Beluga plots within the $C_{phytoplankton}$ lines, and polar bear plots on the steeper C_T enrichment line.

Animals spanned a range from 100% C_M to 100% C_T when both phytoplankton and MPB was used as the marine end-member in the IsoError model. When phytoplankton was used as the marine end-member, approximately 75% of lagoon genera (31 out of 40 taxa) had C_T values of 0% (**Table 2.4, Fig. 2.6A**). For 9 taxa, C_T values ranged from 1 to 45%. When using MPB as the marine end-member, all lagoon genera showed some reliance on C_T ($C_T > 0\%$) (**Table 2.4, Fig. 2.6B**).

Nearshore invertebrates and fishes showed similar reliance on terrestrial C as congeners collected from the lagoon environment (**Table 2.5**). Specifically, when phytoplankton was used as the marine end-member, 4 out of 11 nearshore genera had C_T values < 1%. When MPB was used as the marine end-member, all invertebrate genera showed some reliance on C_T. Sculpin (*Myoxocephalus*), the only fish that differed between lagoon and nearshore environment was 47 to 80% C_T, in nearshore sites and 0 to 49% C_T at lagoon sites. *Salvelinus* from the Hulahula River were 100% C_T using both

marine end-members, approximately 50% higher than *Salvelinus* from lagoon or nearshore stations.

All three bird species were 0% C_T using $\delta^{13}C_{phytoplankton}$, but showed reliance on C_T when $\delta^{13}C_{MPB}$ was used (*Anser albifrons* 13%, *Gavia adamsii* 37%, and *Somateria mollissima* 44%). For marine mammals, only polar bear showed reliance on C_T (15%) with $C_{phytoplankton}$ as the marine end-member. All mammals showed evidence of significant assimilation of C_T (C_T > 49%) with C_{MPB} as the marine end-member.

DISCUSSION

Sources of organic matter

The quantity and composition of POM in Alaskan Beaufort Lagoons experience strong seasonal variations (Connelly et al. 2015). Specifically, a parallel study on the same lagoons included in the present analysis found that SPOM in August was depleted in ^{13}C (~ -27‰) and had a relatively high proportion of terrestrial fatty acid markers. Although there was high interannual variability in $\delta^{13}C$ and $\delta^{15}N$ values for SPOM (as in Connelly et al. 2015) and BPOM at lagoon and nearshore sites reported here, the means for all years are similar to those reported for other studies located in the coastal eastern Alaskan Beaufort Sea (Dunton et al. 2006, 2012). Therefore, we are confident that the SPOM and BPOM isotopic means reported here are robust and representative of typical open-water lagoon and nearshore values. Interestingly, the agreement of our values with those of Dunton et al. (2012) also suggests that despite the changing coastal environment over the last decade, the bulk composition of OM during summer as reflected in stable isotope values along the coast has not changed substantially.

Analysis of lagoon and nearshore SPOM and BPOM suggest there are at least two distinct sources of OM present in the coastal environment that are distinguishable using C and N stable isotopes: marine primary production (more enriched in ^{13}C and ^{15}N) and terrestrial OM inputs. C_T reaches the coastal environment from watershed runoff and coastal erosion—bluffs on the land margin of the lagoons sampled are actively receding (Jorgenson and Brown 2005). In general, rivers on the North Slope deliver more dissolved OM than particulate OM, unless inputs from the Colville River are considered, but POM inputs from smaller rivers may be an important carbon source for lagoon consumers (McClelland et al. 2014). Erosional and runoff terrestrial sources mix with *in situ* primary production in the coastal environment to produce the intermediate SPOM and BPOM $\delta^{13}C$ and $\delta^{15}N$ values observed in the coastal environment. Marine primary production includes phytoplankton and benthic microalgae, which can be further distinguished based on ^{13}C content [literature values of MPB are more ^{13}C enriched (e.g. Newell et al. 1995) than phytoplankton values reported here].

While primarily comprised of marine phytoplankton, the offshore marine SPOM sample likely included particulate OM from other sources because the SPOM value is 3‰ more enriched than the 20 μm plankton net sample from the same stations. Our SPOM samples likely represent a mixture of material that could include resuspended benthic organic matter, small zooplankton, heterotrophic protists, and fecal pellets and other detritus. The inclusion of resuspended benthic organic matter than has been microbially reworked and/ or microphytobenthos may cause this enrichment. Mid-late summer phytoplankton production is low in lagoons, because of the low inorganic nitrogen concentrations (Dunton et al. 2012), which implies that MPB may be an important C source for biota. MPB, composed mostly of diatoms, is present on ocean sediments, and is likely one component of BPOM values reported here, though it was not

isolated and analyzed separately. Although, no published stable isotope measurements exist for benthic microalgae in the Beaufort Sea, values from other locations range from -13 to -21‰ (France 1995; Newell et al. 1995; Cloern et al. 2002; Kang et al. 2003). Our marine BPOM $\delta^{13}C$ values may reflect a combination of phytoplankton, MPB, and terrestrial particulate carbon as well as marine detritus, bacteria, and small animals such as nematodes and harpacticoid copepods; the values reported here are similar to those reported for the Canadian Beaufort shelf (~ -25‰, Goñi et al. 2000).

Ice algae, which is present in the Beaufort Sea during non-summer months, is a fourth carbon source that can have similar isotope values to that of MPB. Ice POM isotopes have been reported as -17.7‰ in the North Water Polyna (Hobson et al. 2002), -15.7‰ in the Svalbard archipelago (McMahon et al. 2006), and -20.6‰ in the Chukchi Sea (Dunton, unpublished data). Ice algae are not typically found in coastal environments past June, however, and our sampling occurred during the open water period in August. In addition, no ice algae were observed in any of these lagoons during spring 2012 and 2013 (Dunton and McClelland, unpublished results). Consequently its role as a carbon source in these lagoons in August is likely minimal (Connelly et al. 2015).

The intermediate carbon and nitrogen isotope values of SPOM at lagoon and nearshore sites (**Fig. 2.3**) suggest that this OM is comprised of a mixture of marine phytoplankton and suspended particulate C_T. Lagoon and nearshore BPOM were more ^{15}N depleted than marine BPOM and are likely comprised of settled phytoplankton, MPB, and particulate C_T, in addition to detritus, bacteria and small animals. Because C_T is ^{15}N depleted relative to marine OM sources, C_T is likely a large component of BPOM at nearshore and lagoon sites. Even though BPOM may include MPB, it is less ^{15}N enriched than SPOM at both lagoon and nearshore sites, suggesting BPOM includes more

C_T than does SPOM, though this may also be an artifact of processing effects (Macko et al. 1987).

SPOM and BPOM from lagoons and nearshore sites are important food sources for filter-feeding/grazing and deposit feeding biota, respectively. Previous research in these lagoons revealed that in August, lagoon SPOM is characterized by a higher proportion of dinoflagellates relative to diatoms and has a higher polyunsaturated fatty acid content than SPOM from nearshore sites, though lagoon and nearshore SPOM both contained terrestrial material (Connelly et al. 2015). This finding suggests lagoon SPOM is likely an important food source for consumers because of its high nutritional value (Connelly et al. 2015).

Lagoons vs. nearshore faunal comparison

Consistent with similarities in isotope values for POM between lagoon and nearshore sites, five faunal taxa exhibited no difference between lagoon and nearshore sites, indicating that there are no differences in selective feeding for these organisms between sites. The four taxa (*Gammarus*, *Lumpenus*, *Boreogadus*, *Salvelinus*) that were more enriched at nearshore stations in both ^{13}C and ^{15}N likely reflect greater reliance on C_M relative to their counterparts in the lagoons.

Dunton et al. (2006) found that Arctic cod were at least 3‰ more depleted in ^{13}C and ^{15}N in lagoons relative to the nearshore environment, and conclude that these depleted values provide the most compelling evidence that terrestrially derived carbon is important to lagoon food webs. The authors note, however, that cod's expected prey items, amphipods and mysids, from lagoons did not exhibit this depletion. Dunton et al. (2012) examined a wider range of organisms from the Alaskan Beaufort and found that all taxa from the Beaufort Sea shelf were more ^{13}C enriched than from lagoons, and that

most taxa from the shelf were also enriched in ^{15}N. They concluded this offshore enrichment reflected greater reliance on C_M (Dunton et al. 2012). Our results likely differ because Dunton's shelf taxa were collected across the Beaufort Sea shelf and further offshore than those in this study. This would suggest a gradient where C_T becomes less important as consumers move offshore.

Motile organisms can travel between lagoon and open water areas, For example, mysids and amphipods are known to migrate between lagoons and nearshore waters (Craig 1984). Phytoplankton may also be advected into lagoons through channels. Craig and others argue that these processes are necessary to account for the high invertebrate biomass observed in lagoons (1984). These movements would further blur any differences in C_T and C_M assimilation, should they exist, between our lagoon and nearshore sites.

Food web structure

As expected, our food web analysis shows that lagoon and nearshore consumers assimilated a range of carbon sources. Primary consumers can consume phytoplankton, microphytobenthos (MPB), and terrestrially derived OM, all of which may be present in suspended POM, and/ or surface sediments. Selective feeding on and/or assimilation of particular C sources may contribute to the observed variations in ^{13}C at the second trophic level. A high degree of selectivity by upper TL organisms would maintain differences in $\delta^{13}C$, whereas generalist, omnivorous feeders would re-integrate the diverse ^{13}C signals and reduce ^{13}C variability. Connelly et al (2015) reports that invertebrates contained large contributions from bacterial fatty acids, suggesting that a depleted ^{13}C signal in lower trophic invertebrates (i.e. TL < 3) may reflect either the direct consumption of terrestrially-derived OM or indirect C_T consumption via bacterial food webs.

In the Arctic, omnivory is the rule rather than the exception (Dunton and Schell 1987) and, as in other marine environments, true herbivores are rare, so it is not surprising that the range of $\delta^{13}C$ values decreased with increasing trophic level. All invertebrates were more enriched in ^{13}C relative to lagoon/ nearshore SPOM and BPOM, suggesting the occurrence of post-photosynthetic carbon fractionation. Other Arctic studies, including those in the Beaufort Sea, have also found benthic invertebrates to be more ^{13}C enriched than marine POM (Dunton et al. 1989; Hobson et al. 1995; McTigue & Dunton 2014, Connelly et al. 2014). There are three potential explanations for this enrichment, besides the occurrence of step-wise trophic level enrichments.

First, it may suggest that invertebrates were selectively (passively or actively) incorporating phytoplankton production, which is more enriched in ^{13}C and ^{15}N than all lagoon/ nearshore POM samples. Connelly et al. (2014) suggest that zooplankton in the Beaufort Sea (e.g. mysids and amphipods), even those associated with the seafloor, selectively consume marine phytoplankton. Other filter feeders analyzed in this study may selectively consume marine phytoplankton as well, which would explain their enriched ^{13}C and ^{15}N values relative to POM (**Fig. 2.5B**). Secondly, some animals may preferentially consume MPB, which can equal or exceed phytoplankton production in shallow (<30 m) Arctic environments (Glud et al. 2009). Most subsurface/ deposit feeders and some epibenthic consumers had more enriched $\delta^{13}C$ values than would be expected for an organism feeding 100% on marine phytoplankton (**Fig. 2.5A**), suggesting they consume significant amounts of MPB. A third explanation is that this ^{13}C enrichment may reflect assimilation of microbially-reworked organic matter, because microbial processes often result in isotopically-enriched OM (Macko et al. 1987). This explanation has been proposed to explain ^{13}C enrichment of fauna relative to phytoplankton in the Bering and Chukchi Sea (McConnaughey and McRoy 1979,

Hobson et al. 1995, Lovvorn et al. 2005, McTigue and Dunton 2014, McTigue et al. 2015) and for ^{13}C enrichment of BPOM relative to SPOM in near-bottom waters near Spitsbergen and on the Beaufort Sea shelf (Tamelander et al. 2006, Connelly et al. 2012).

In general, the stable isotope compositions and the derived trophic level of invertebrate prey species agree with previous isotope work in the Arctic (e.g. Dunton et al. 1989; Hobson & Welch 1992; Dunton et al. 2006; Dunton et al. 2012; Hobson et al. 2002; Iken et al. 2005; Iken et al. 2010). Because benthic biota in eastern Alaskan Beaufort lagoons are well-studied, we focus here on larger animals and upper TL consumers, and consider benthic invertebrates as potential prey items.

Insights into individual species feeding ecology

Many of the upper level trophic species included in this study are noted for their importance to subsistence hunters across the eastern Beaufort Sea coast or have been cited as critical trophic links in coastal food webs across the Arctic. Here, we focus on the most ubiquitous upper TL consumers that have been traditionally harvested by native residents of North Slope villages, especially Kaktovik, or are noted as key species in the coupling of benthic and pelagic production.

Salvelinus spp. – Arctic char and Dolly varden

We combined the isotopic data for both Arctic char (*Salvelinus alpinus*) and Dolly varden (*Salvelinus malma*), which are often difficult to distinguish in the field. Both are anadromous and migrate from streams to coastal waters to feed during summer and return to streams in September to spawn and overwinter (Schmidt et al. 1983a). Juvenile Arctic char sampled from the Hulahula River, which may have been young-of-the-year, were 100% reliant on $C_{T,}$ as expected for fishes that have never entered the marine environment and therefore feed exclusively in the terrestrial environment. Larger adult

Salvelinus (~ 70 cm) sampled from lagoon and nearshore waters occupied a higher trophic level (TL 2.8, TL 3.2) and were less reliant on C_T than the river fish, but still showed significant consumption of terrestrially-derived OM (C_T = 12 to 67%).

Salvelinus spp. typically feed on small fish, crustaceans, and aquatic insects when inhabiting tundra streams and on benthic invertebrates (mainly amphipods and mysids) when inhabiting lagoon and nearshore waters (Craig and Haldorson 1981, Harris 1993). The river juveniles consume mostly aquatic insects, such as *Chironomids*, whereas the adults collected from lagoon and nearshore waters probably fed more on marine invertebrates, which explains the differences in %C_T and TL observed.

Though Jobling et al. (1998) reported that younger Arctic char contain more lipids in their muscle tissue than adults, it is unlikely that differences in lipid content led to the observed differences in %C_T because fish sampled from all sites had similar C:N molar ratios (3.9 to 4.5). It is also possible that the high reliance on C_T observed in adult fish may be a carry-over from their river residence if the turnover time of char muscle is greater than their time occupying lagoons. The muscle tissue turnover time for char has not been determined, but results for other fishes show the half-life for carbon in muscle tissue ranges from 8 to 173 days, depending mostly on fish size and growth rate (Weidel et al. 2011, Vander Zanden et al. 2015). The impact of tissues built while in the freshwater environment on our results for lagoon and nearshore fish is impossible to quantify without experimental studies on muscle turnover rates, but cannot be discounted. Overall, the results for river vs. coastal (lagoon and nearshore) char show that the IsoError model can accurately identify fish that rely heavily on C_T as a basal diet source.

Myoxocephalus spp. – Sculpin

Sculpin are marine fishes that move from deeper, offshore waters to coastal Beaufort waters to feed during the summer. Their diet consists mainly of small peracarid

crustaceans (amphipods, isopods, mysids) and molluscs (Schmidt et al. 1983b). Sculpin are becoming an increasingly important diet component for Arctic shorebirds; for example black guillemots at Cooper's Islands consume less of their preferred prey, Arctic cod, and more sculpin because decreased sea ice extent has led to decreases in late summer cod abundance (Divoky et al. 2015). In this study, lagoon sculpin appear to incorporate more C_M than C_T (C_T = 0 to 49%). This is consistent with previous isotope studies, which concluded sculpin rely on a marine phytoplankton carbon source across the Beaufort Sea (sculpin values range from -20.5 - 23.0‰; Schell 1983; Loseto et al. 2008; Dunton et al. 2012). Conversely, sculpin collected from the nearshore environment appear to consume more C_T than C_M (C_T = 47 to 80%).

This apparent difference in basal carbon source may be related to the size and life history stage of individuals sampled. Nearshore sculpin were smaller (total length < 5 cm) than those collected from lagoons (total length 7 - 23 cm). Linear regression analysis revealed a significant positive linear relationship between both isotopes and total length in sculpin (**Fig. 2.7**), which suggests that sculpin shift their diet ontogenetically. This relationship suggests that smaller sculpin consume more C_T, but greater lipid-content may also cause smaller fish to be more ^{13}C depleted. Younger fishes tend to contain more fats in their muscles than adult organisms (Jobling et al. 1998, Kiessling et al. 2001), which agrees with C:N values reported here (5.1 for small nearshore fish, and 4.2 for larger, lagoon fish). Juvenile sculpin may also feed more on lipid-rich copepod nauplii (Scott et al. 2000), whereas adult sculpin feed mostly on peracarid crustaceans, such as mysids and amphipods, which store less lipids than copepods such as *C. hyperboreus* (Connelly et al. 2012).

Coregonus spp. – Arctic cisco and least cisco

Cisco (*Coregonus* spp.) are one of the most important fishes to subsistence fisheries on the Beaufort coast (Schmidt et al. 1983b). Ciscos are anadromous, where young-of-the-year migrate from rivers to estuarine lagoons during the spring break-up period, spending the summer open-water period in coastal waters, and returning to river deltas in the fall to spawn and/or overwinter (Schmidt et al. 1983b). Ciscos prefer the shallower, warmer waters of lagoons to the Beaufort Sea shelf (Truett 1984). The feeding ecology of cisco and previous isotopic work suggest terrestrial matter is an important basal carbon source for cisco (Schell 1983). All life history stages of cisco forage in nearshore Beaufort Sea waters during the summer, feeding on mysids (70% of their summer diet), amphipods, and polychaetes and may travel up streams to forage on aquatic invertebrates, such as chironomids (Schmidt et al. 1983b). Schell (1983) showed that coregonids consume C_T derived material while overwintering in Arctic streams, but are indistinguishable from marine fishes during their summer lagoon occupation. Our models show 0 to 61% of cisco (*Coregonus autumnalis, Coregonus sardinella*) carbon is derived from C_T, suggesting C_T may be an important basal source. Though only a few amphipod and polychaete species sampled in this study showed evidence of incorporating C_T, if the cisco supplemented their diet with aquatic insects, this would explain the depleted $\delta^{13}C$ values and resulting $\%C_T$ values observed here.

Boreogadus saida – Arctic cod

Arctic cod are the dominant marine fish in Beaufort Sea waters in terms of abundance and biomass, and have been hailed as a vital link between benthic production and more pelagic, upper level consumers (e.g., Craig & Haldorson 1981; Bradstreet & Cross 1982; Dehn et al. 2007). In the Beaufort Sea, mammalian and bird predators consume approximately 28,630 MT of Arctic cod annually (Frost and Lowry 1984). In the Alaskan Beaufort Sea, Arctic cod typically aggregate in nearshore and lagoon waters

during the end of the open-water period (Truett 1984). In the coastal Beaufort, Arctic cod are small (< 30 cm) and consume a variety of benthic invertebrates and pelagic zooplankton, though they feed mainly on *Calanus* copepods (Truett 1984). In the Canadian Beaufort Sea, young-of-the-year (< 2 cm) feed mainly on copepods and eggs, whereas juveniles and adults (> 2 cm) include more invertebrates, such as amphipods, mysids, and small fish into their diets (Walkusz et al. 2011). The Arctic cod collected in this study were between 3 and 7 cm in total length, and thus consume a mix of zooplankton and benthic invertebrates. *Calanus* copepods appear to be an extremely important diet component for Arctic cod, since these copepods are the only prey item more depleted in ^{13}C than Arctic cod themselves **(Tables 2.4, 2.5, Fig. 2.4**). Their intermediate trophic level (2.6 to 2.7) suggests invertebrates are potential prey items, though, the paucity of more ^{13}C-depleted invertebrates implies Arctic cod are either feeding exclusively on copepods or are consuming other invertebrates not sampled in our study.

We found that C_T is a major carbon source for Arctic cod (30 - 70% C_T), confirming the findings of Dunton et al. (2006), who calculated that ~50 to 70% of Arctic cod carbon was of terrigenous origin. We also corroborate the claim that cod are an important link between lower and upper level consumers (see following section). In addition to cod, *Lumpenus fabricii* also displayed heavy reliance C_T (25 to 70%), another example of the dependence of Beaufort fishes on C_T.

Marine mammals

Although we analyzed only muscle tissue from marine mammals, the turnover time of muscle in large mammals may be longer than that of smaller fish and invertebrates (Vander Zanden et al. 2015). The half-life of ^{13}C in captive cetaceans is 11-

23 days (Browning et al. 2014), therefore, we are reasonably confident the data presented here is representative of the mammal's diet during the summer open water period.

Bearded seal (*Erignathus barbatus*) showed isotopic evidence of consuming moderate amounts of C_T-derived material (0 to 49% C_T). Bearded seal forage in the coastal Beaufort and are known to consume large amounts of Artic cod under certain circumstances, but more common prey items include molluscs and crustaceans (Dehn et al. 2007), which did not have a large %C_T values. The individual we sampled likely consumed a mix of Arctic cod and marine invertebrates.

Bowhead whales (*Balaena mysticetus*) typically spend the summer open-water period and early fall foraging in the inner-shelf of the Beaufort Sea (Lowry and Burns 1980, Moore et al. 2000). Bowheads captured near Kaktovik are non-selective filter feeders and the majority of their diet is comprised of zooplankton (mostly *Calanus hyperboreus*), though benthic invertebrates such as mysids, pelagic amphipods, and small fish are also consumed (Lowry and Burns 1980). We show that bowheads occupy a lower TL than other marine mammals, which reflects their consumption of copepods and agrees with previous work on marine mammals in the Beaufort Sea (Hoekstra et al. 2002). Bowheads derive from 0 to 60% of their carbon from C_T, which is a reasonable value for a diet based mainly on nearshore *Calanus* (48 to 80% C_T) that may include some nearshore invertebrates and small fish (C_T range: 0 to 80%). It should be noted, however, that *Calanus* copepods contain large amounts of lipids, indicated by their elevated C:N value of 9, which are inherently depleted in ^{13}C, so it is likely that both IsoError model runs overestimate their reliance on C_T.

Small belugas (*Delphinapterus leucas*) feed in nearshore Beaufort waters during ice-free months (Loseto et al. 2009). Belugas consume primarily Arctic cod (80% of their total diet) during their summer occupation of the Beaufort Sea coast, though they also

consume other fish (ciscoes and sculpin) and benthic invertebrates depending on age and sex (Frost and Lowry 1984, Loseto et al. 2009). Arctic cod and cisco sampled in this study both had high %C_T values (*Boreogadus* 36 to 76%, *Coregonus* 0 to 61%), which explains our finding that 0 to 60% of beluga carbon originated from terrestrial sources, despite other common prey items, such as Saffron cod (*Eleginus*) (Frost and Lowry 1984), incorporating only small amounts of C_T.

Polar bears (*Ursus maritimus*) are a top Arctic carnivore that hunt and scavenge opportunistically. The male individual sampled here (1-3 years old) occupied TL 4.7, which agrees with previous isotopic work on Beaufort polar bears (Bentzen et al. 2007). Ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) are consumed primarily in the winter and spring and are the main prey items for polar bears in the study area (Herreman and Peacock 2013). In summer, polar bears consume a wide variety of marine (marine algae, fish, whale carcasses, seal, and waterfowl) and terrestrial based food (berries, caribou, ptarmigan, bird eggs) (see review in Gormezano & Rockwell 2013).

The high reliance on C_T (15 to 68%) we report may be in part due to consumption of terrestrial prey items. It could also be the result of consuming fish (a commonly reported prey items for polar bears in all regions of the Arctic) that rely on C_T, such as Arctic char and Arctic cod. Another important food source may be scavenging whale carcasses, usually bowhead, at bone piles created after subsistence hunts in villages on the North Slope (Miller et al. 2004, Herreman and Peacock 2013). One such bone pile in located outside the village of Kaktovik on Barter Island, within our study area, which may act as a persistent and reliable food source to polar bears (Bacon et al. 2009). The bowheads and belugas in this study showed potential reliance on C_T, therefore the inclusion of whale carcasses in a polar bear's diet may explain the high reliance on C_T

reported here. This result is significant because it suggests that a top Arctic carnivore is consuming prey items that are either within or directly associated with coastal lagoon systems.

The time available for polar bears to forage on these seals and other marine mammals before the bear's landward migration is decreasing because spring ice breakup is occurring earlier due to climate warming (Galley et al. 2008), This change makes their summer diets during their land residence increasingly important. Bears in Hudson Bay, Canada are consuming more terrestrial food sources, such as snow geese and caribou, now than in the past (Gormezano and Rockwell 2013, Iles et al. 2013), though this trend has not been demonstrated elsewhere in the Arctic (Rode et al. 2015). Rode et al. (2015) also concluded that polar bears cannot meet their physiological nutrient needs with a solely terrestrial diet.

Birds

While we assume the isotopic value of birds inhabiting Beaufort lagoons in August is reflective of their summer diets, the species we examined are migratory and the exact timing of their migration is unknown. Therefore, the isotopic value of their tissue could represent feeding before they reached the Beaufort coast. To eliminate this source of error, future studies should examine fledgling birds.

All birds we examined showed low reliance on C_T. The white fronted goose (*Anser albifrons*) mostly herbivorous in the summer, but forages on bivalves, marine and aquatic worms, and aquatic insects (Derksen et al. 1982). Surprisingly, the individual we sampled showed only slight reliance on terrestrially-derived material (C_T = 0 to 10%). Perhaps this individual fed more on bivalves and marine worms than is typical for geese, or consumed a more ^{13}C enriched terrestrial C source that was not sampled. Although yellow-billed loons (*Gavia adamsii*) are fish-specialists that have been reported to

consume Arctic cod as 50% of their diet in the Beaufort Sea, they also consume crustaceans, molluscs, and annelids (Frost and Lowry 1984). The loon we sampled showed reliance on C_T to be low (0 to 30%), therefore it is unlikely it preyed this extensively on cod. Common eiders (*Somateria mollissima*) build nests on barrier islands during the summer and consume zooplankton (mostly *Calanus*), molluscs, crustaceans, and small fish (Frost and Lowry 1984). We show eiders derive 0 to 44% of their carbon from C_T. The inclusion of *Calanus hyperboreus* and small fish, which both show evidence of incorporating C_T, in their diet might explain the 2‰ depletion of eiders relative to the other birds sampled and slightly higher reliance on C_T. Because of the limited sample size of this study, it is difficult to draw broad conclusions about shorebird feeding ecology.

Conclusions

While terrestrial contributions to food webs have been well defined in temperate estuaries, their role in Arctic food webs has been given far less attention. This study builds on work from the last decade to assess the role of terrestrial carbon in Arctic coastal food webs. Seventeen out of 51 genera analyzed showed reliance on C_T (i.e. $C_T \geq 1\%$) when the marine phytoplankton end-member was used (**Fig. 2.5**), which corroborates previous studies that found benthic food webs are supported by terrestrial carbon subsidies. When MPB is used as the marine end-member, 51 out of 51 genera showed reliance on C_T. These findings confirm that C_T is an important, if minor, subsidy in Arctic coastal waters.

We provide compelling evidence for the transfer of C_T from benthic food webs to upper level consumer species, such as beluga whales, bowhead whales, and polar bears,

that are important ecologically as well as to the subsistence diet and cultural identity of North Slope Inupiat communities. Arctic cod, which are known to be a key link between benthic and pelagic organisms, have the potential to be vital in the transfer of C_T subsidies to upper trophic levels, because all animals known to feed heavily on cod showed a high reliance on C_T when both marine end-members were used in the IsoError model. However, more research is needed that examines multiple terrestrial biomarkers to determine this link conclusively.

Climate change is predicted to alter carbon sources in the Alaskan Beaufort in several ways, which may in turn affect the relative amounts of energy sources available to coastal food webs. Overall marine primary productivity, which is tightly coupled to sea ice cover, will likely increase (Arrigo et al. 2008), but the balance between benthic (MPB) and pelagic (phytoplankton) production may change (Glud et al. 2009). Terrestrial inputs will be affected by changing river inputs (Peterson et al. 2006), decreased glacial runoff (Nolan et al. 2011), and increased coastal erosion due a longer open water period, larger areas of open water, increased storminess, and decreased permafrost (Overeem et al. 2011, Barnhart et al. 2014). It is not yet clear if these combined phenomenon will ultimately result in increased or decreased delivery of allochthonous C_T to lagoons or how this may affect *in situ* lagoon production. Increased C_T inputs may lower production because erosional processes are often associated with higher water turbidity (Glud et al. 2009), or this terrestrial OM may be readily consumed by lagoon invertebrates. We show that some terrigenous OM, which is incorporated into benthic invertebrates, is also transferred to upper trophic levels. As such, these larger animals will likely be affected by aspects of climate change that affect land-sea coupling as well those that cause sea-ice loss.

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Table 2.1 Locations (decimal degrees) and data from *in situ* sensor measurements (mean ± SE (n)) taken at sites along the eastern Alaska Beaufort Sea coast.

Sensor data are means of surface (< 1 m) measurements obtained in August at two-three stations in each lagoon and nearshore sites. Marine sites are a single measurement obtained in August 2014. Several stations at each river site were visited in August 2011 (Hulahula River) or August 2012 (Jago River), though sensor data was not obtained. "-" indicates data was not collected.

Site Type	Site	Site Code	Latitude (°N)	Longitude (°W)	Temp (°C)	Salinity	Bottom Depth (m)	Years Sampled
Marine	STA 21	-	70.28	-143.91	-	36 (1)	37	2014
	STA 22	-	70.19	-142.90	-	36 (1)	35	2014
	STA 24	-	70.26	-141.76	-	35 (1)	52	2014
	STA 25	-	69.85	-141.72	-	34 (1)	23	2014
Nearshore	Hulahula Delta	HU	70.07	-144.19	6.2 ± 0.7 (4)	27.7 ± 1.9 (4)	4	2011, 2012
	Bernard Spit	BE	70.16	-143.58	6.4 ± 0.5 (6)	26.6 ± 1.6 (6)	10	2011, 2012, 2013
	Demarcation Point	DP	69.70	-141.31	4.1 ± 1.1 (4)	23.7 ± 4.4 (4)	6	2011, 2012
Lagoon	Kaktovik	KA	70.09	-143.61	11.6 ± 0.4 (9)	23.2 ± 0.8 (9)	4.5	2011, 2012, 2013
	Jago	JA	70.11	-143.50	9.9 ± 0.4 (9)	23.5 ± 1 (9)	4	2011, 2012, 2013
	Angun	AN	69.96	-142.49	10.3 ± 1.1 (6)	22.6 ± 2 (6)	2.5	2011, 2012, 2013
	Nuvagapak	NU	69.86	-142.19	10.1 ± 0.6 (6)	11 ± 3.5 (6)	2.5	2011, 2012
River	Hulahula River	HU-R1	69.49	-144.36	-	-	-	2011
		HU-R2	69.76	-144.16	-	-	-	2011
		HU-R3	69.98	-144.02	-	-	-	2011
	Jago River	JA-R	69.72	-143.60	-	-	-	2012

Table 2.2 Mean (± SE) $\delta^{13}C$, $\delta^{15}N$, and C:N (molar ratio) of suspended particulate organic matter (SPOM) and benthic particulate organic matter (BPOM) per year, and overall mean for each site type: lagoon, nearshore, marine and river. *n* is the number of samples analyzed for each parameter. "nd" indicates data were not collected.

	SPOM				BPOM			
	n	$\delta^{13}C$ (‰)	δ^{15} N (‰)	Molar C:N	*n*	$\delta^{13}C$ (‰)	δ^{15} N (‰)	Molar C:N
Marine								
2014	4	-21.9 ± 0.6	8.9 ± 1.9	nd	4	-25.6 ± 0.2	4.8 ± 0.5	10.6 ± 1.2
Nearshore								
2011	3	-23.0 ± 0.3	7.5 ± 0.4	6.3 ± 0.2	1	-26.3	2.6	10.1
2012	3	-28.5 ± 0.3	5.8 ± 1.1	7.1 ± 0.3	1	-25.9	2.8	8.1
2013	1	-27.5	9.4	5.9	1	-25.1	3	13.7
mean	7	-26.0 ± 1.1	7.1 ± 0.7	6.6 ± 0.2	3	-25.8 ± 0.4	2.8 ± 0.1	10.6 ± 1.6
Lagoon								
2011	4	-24.8 ± 0.7	6.7 ± 0.4	6.6 ± 0.3	4	-27.2 ± 0.3	3.4 ± 0.2	14.1 ± 0.7
2012	4	-28.9 ± 0.6	5.5 ± 0.9	7.2 ± 0.1	4	-27.7 ± 0.8	3.0 ± 0.2	14.9 ± 1.5
2013	3	-28.3 ± 0.3	7.0 ± 0.8	7.7 ± 0.1	3	-27.0 ± 0.4	3.0 ± 0.4	14.0 ± 0.2
mean	11	-27.2 ± 0.7	6.3 ± 0.4	7.1 ± 0.2	11	-27.3 ± 0.3	3.2 ± 0.2	14.4 ± 0.6
River								
2011	3	-29.3 ± 0.4	3.6 ± 0.5	11.4		nd	nd	nd
2012	1	-28.2	2.5	10.9		nd	nd	nd
mean	4	-29.0 ± 0.5	3.3 ± 0.5	11.1 ± 0.2		nd	nd	nd

Table 2.3 Mann-Whitney U test statistics for comparison of $\delta^{13}C$ and $\delta^{15}N$ values between suspended particulate organic matter (SPOM) and benthic particulate organic matter (BPOM).
Both sources of organic matter were sampled in August from all three site types. SPOM and BPOM differed significantly in $\delta^{13}C$ signal at lagoon and marine sites; SPOM and BPOM different significantly in $\delta^{15}N$ at all site types.

	Site Type	*p*-value	Mann-Whitney U
$\delta^{13}C$	Lagoon	0.532	84
	Nearshore	0.99	13
	Marine	0.029	0
δ^{15} N	Lagoon	<0.0001	6
	Nearshore	0.0091	0
	Marine	0.029	0

Table 2.4 Mean (± SE) $\delta^{13}C$, $\delta^{15}N$, C:N (molar ratios), derived trophic level (TL) and % terrestrial carbon calculated using phytoplankton carbon (% C_T A) and microphytobenthos carbon (% C_T B) as the marine endmember for taxa collected in August from four lagoons (Kaktovik, Jago, Angun, and Nuvagapak) using benthic grabs and trawl nets.
* Indicates a composite comprised of several individuals. Data from all years (2011 - 2014) are combined. Trophic guild shows feeding method (De = deposit, Su = suspension/ filter feeder, Om = omnivore) and location (EB = epibenthic, SR = surface, SS = subsurface).

	n	$\delta^{13}C$ (‰)	δ^{15} N (‰)	Molar C:N	TL	% C_T (A)	% C_T (B)	Trophic Guild
Annelida								
Ampharete finmarchica	2*	-21.4 ± 1.1	8.1 ± 0.7	5.6 ± 0.1	1.2 ± 0.2	0 ± 27	44 ± 10	De/SR
Cistenides spp.	1*	-20.2	8.9	7.4	1.4	0 ± 26	35 ± 10	De/SR
Nereimyra aphroditoides	2*	-19.5 ± 0.3	10.7 ± 0.2	8.2 ± 1	1.9 ± 0	0 ± 14	34 ± 5	De/SS
Prionospio cirrifera	3*	-20.2 ± 0.7	10.2 ± 0.4	6.2 ± 0.3	1.8 ± 0.1	0 ± 19	39 ± 8	De/SR
Terebellides stroemii	6*	-20.3 ± 0.4	10.1 ± 0.3	5.9 ± 0.3	1.7 ± 0.1	0 ± 14	40 ± 5	De/SR
Arthropoda								
Atylus carinatus	1	-21.4	9.6	8.6	1.6	0 ± 24	47 ± 9	Om/EB
Calanus hyperboreus	3*	-23.1 ± 0.4	11.0 ± 1.3	6.1 ± 0.9	2.0 ± 0.4	10 ± 10	66 ± 4	Su/EB
Diastylis spp.	2*	-21.6 ± 0.1	12.4 ± 0.3	9.6 ± 0.6	2.4 ± 0.1	0 ± 7	57 ± 3	Om/EB
Gammaracanthus loricatus	1	-20.4	11.3	8	2.1	0 ± 25	43 ± 9	Om/EB
Gammarus spp.	7*	-20.9 ± 0.7	9.4 ± 0.4	7.2 ± 0.4	1.5 ± 0.1	0 ± 19	43 ± 7	Om/EB
Monoporeia affins	1	-25.0	9.6	8.3	1.6	45 ± 23	79 ± 9	De/SR
Mysis spp.	18*	-19.6 ± 0.5	9.4 ± 0.5	6.7 ± 0.3	1.5 ± 0.1	0 ± 17	31 ± 6	Om/EB
Onisimus glacialis	8*	-19.9 ± 0.8	10.3 ± 0.7	11 ± 1.2	1.8 ± 0.2	0 ± 22	37 ± 8	Om/EB
Pontoporeia femorata	8	-17.7 ± 0.5	9.4 ± 0.2	9.4 ± 0.8	1.5 ± 0.1	0 ± 20	15 ± 6	De/SR
Saduria entomon	5	-19 ± 0.5	12 ± 0.6	9.3 ± 0.8	2.3 ± 0.2	0 ± 17	33 ± 6	Om/EB
Weyprechtia spp.	1	-17.1	12.4	7.8	2.4	0 ± 28	18 ± 10	Om/EB

Table 2.4 Continued

	n	$\delta^{13}C$ (‰)	δ^{15} N (‰)	Molar C:N	TL	% C_T (A)	% C_T (B)	Trophic Guild
Bryozoa								
Alcyonidium disciforme	12*	-22.9 ± 0.6	10.3 ± 0.2	7.5 ± 1	1.8 ± 0.1	2 ± 14	63 ± 6	Su/EB
Eucratea loricata	3	-22.8 ± 2.1	8.5 ± 0.8	7.6 ± 1.7	1.3 ± 0.2	0 ± 49	57 ± 19	Su/SR
Cephalorhyncha								
Halicryptus spinulosus	7*	-19.8 ± 0.6	12.1 ± 0.6	5.8 ± 0.3	2.3 ± 0.2	0 ± 18	40 ± 7	De/SS
Priapulus caudatus	17*	-18.3 ± 0.3	12.5 ± 0.3	4.7 ± 0.1	2.4 ± 0.1	0 ± 15	28 ± 5	De/SS
Mollusca								
Cylichna alba	14	-17.5 ± 0.4	10.6 ± 0.3	5.9 ± 0.2	1.9 ± 0.1	0 ± 19	16 ± 6	De/SR
Liocyma fluctuosa	17*	-22.2 ± 0.5	8.8 ± 0.2	5.8 ± 0.2	1.3 ± 0.1	0 ± 13	52 ± 5	Su/SR
Macoma moesta	1*	-22.4	8.6	9	1.3	0 ± 24	54 ± 9	De/SR
Portlandia arctica	3*	-21.2 ± 1.3	10.3 ± 0.9	5.4 ± 1.4	1.8 ± 0.3	0 ± 32	48 ± 12	De/SS
Chordata								
Molgula griffithsii	1*	-23.5	8.1	9.6	1.1	1 ± 24	62 ± 9	Su/EB
Fish								
Boreogadus saida	4*	-24.1 ± 0.4	11.6 ± 0.4	4.6 ± 0.4	2.2 ± 0.1	37 ± 11	76 ± 5	Om/EB
Coregonus spp.	4*	-21.9 ± 0.3	13.2 ± 0.3	4.3 ± 0.2	2.6 ± 0.1	0 ± 10	61 ± 4	Om/EB
Eleginus gracilis	3	-18.9 ± 0.1	15.2 ± 0.4	3.7 ± 0	3.2 ± 0.1	0 ± 11	40 ± 4	Om/EB
Lumpenus fabricii	12	-23.7 ± 0.6	12.1 ± 0.3	4.8 ± 0.1	2.3 ± 0.1	32 ± 15	74 ± 6	Om/EB
Myoxocephalus spp.	8	-20.1 ± 0.4	14.6 ± 0.6	4 ± 0.1	3.1 ± 0.2	0 ± 12	49 ± 5	Om/EB
Pleuronectes glacialis	10	-19.6 ± 0.5	12.6 ± 0.7	4.3 ± 0.2	2.5 ± 0.2	0 ± 16	40 ± 6	Om/EB
Salvelinus spp.	7	-22.3 ± 1.1	13.9 ± 0.6	4.5 ± 0.3	2.8 ± 0.2	13 ± 25	67 ± 10	Om/EB

Table 2.5 Mean (± SE) $\delta^{13}C$, $\delta^{15}N$, C:N (molar ratios), derived trophic level (TL) and % terrestrial carbon calculated using phytoplankton carbon (% C_T A) and microphytobenthos carbon (% C_T B) as the marine end-member for taxa collected in August from rivers (2012) and nearshore (2011-2014) sites using benthic grabs, trawl nets, and opportunistic collections from local hunters and fishers.

Data from all years are combined. * Indicates a composite comprised of several individuals. Trophic guild (invertebrates and fish only) shows feeding method (De = deposit, Su = suspension/ filter feeder, Om = omnivore) and location (EB = epibenthic, SR = surface, SS = subsurface).

	n	$\delta^{13}C$ (‰)	δ^{15} N (‰)	Molar C:N	TL	% C_T (A)	% C_T (B)	Trophic Guild
Phytoplankton (20um net)	4*	-24.6 ± 0.9	7.6 ± 1.5	n/a	1.1 ± 0.4	n/a	n/a	n/a
Nearshore invertebrates								
Arthropoda								
Calanus hyperboreus	2*	-24.8 ± 1.2	10.2 ± 0.2	8.7 ± 1.3	1.9 ± 0.1	48 ± 27	80 ± 11	Su/EB
Gammarus spp.	1*	-19.5	10.5	5.1	2.0	0 ± 26	35 ± 10	Om/EB
Mysis spp.	3*	-20.3 ± 0.7	9.5 ± 0.3	6.5 ± 0.9	1.7 ± 0.1	0 ± 19	39 ± 7	Om/EB
Bryozoa								
Eucratea loricata	1*	-24.6	13.4	12.8	2.8	64 ± 23	86 ± 9	Su/SR
Cephalorhyncha								
Priapulus caudatus	1*	-22.5	10.9	7.3	2.1	0 ± 24	62 ± 9	De/SS
Cnidaria								
Gersemia rubiformis	1	-23.6	11.4	6.8	2.3	29 ± 23	73 ± 9	Su/EB
Mollusca								
Portlandia arctica	4*	-17.8 ± 0.5	9.2 ± 0.1	5.3 ± 0.3	1.6 ± 0	0 ± 21	17 ± 7	De/SS
Nearshore fish								
Boreogadus saida	5	-23.6 ± 0.5	12.6 ± 0.3	4.7 ± 0.1	2.6 ± 0.1	36 ± 12	75 ± 5	Om/EB
Lumpenus fabricii	1	-22.8	13.5	4.3	2.9	25 ± 23	71 ± 9	Om/EB

Table 2.5 Continued

	n	$\delta^{13}C$ (‰)	δ^{15} N (‰)	Molar C:N	TL	% C_T (A)	% C_T (B)	Trophic Guild
Myoxocephalus spp.	6	-24.1 ± 0.4	12.4 ± 0.4	5.1 ± 0.2	2.6 ± 0.1	47 ± 10	80 ± 4	Om/EB
Salvelinus spp.	1	-21.9	14.5	3.9	3.2	12 ± 23	66 ± 9	Om/EB
River fish								
Salvelinus alpinus	2*	-27.9 ± 0.2	5.9 ± 0.2	4.4 ± 0.2	1.9 ± 0.1	100 ± 11	100 ± 4	Om/EB
Birds								
Anser albifrons	1	-17.6	8.5	6.7	1.4	0 ± 29	13 ± 10	-
Gavia adamsii	1	-18.1	16.3	4.7	3.7	0 ± 25	37 ± 10	-
Somateria mollissima	1	-21.7	6.6	4.0	0.9	0 ± 25	44 ± 9	-
Mammals								
Balaena mysticetus	3	-21.0 ± 0.4	13.0 ± 0.2	4.5 ± 0.1	2.8 ± 0.1	0 ± 24	60 ± 9	-
Delphinapterus leucas	3	-19.8 ± 0.3	18.3 ± 1.5	4.6 ± 0.8	4.3 ± 0.4	0 ± 11	57 ± 4	-
Erignathus barbatus	1	-19.1	17.3	4.2	4.0	0 ± 24	49 ± 9	-
Ursus maritimus	1	-20.4	20.2	4.1	4.9	15 ± 23	68 ± 9	-

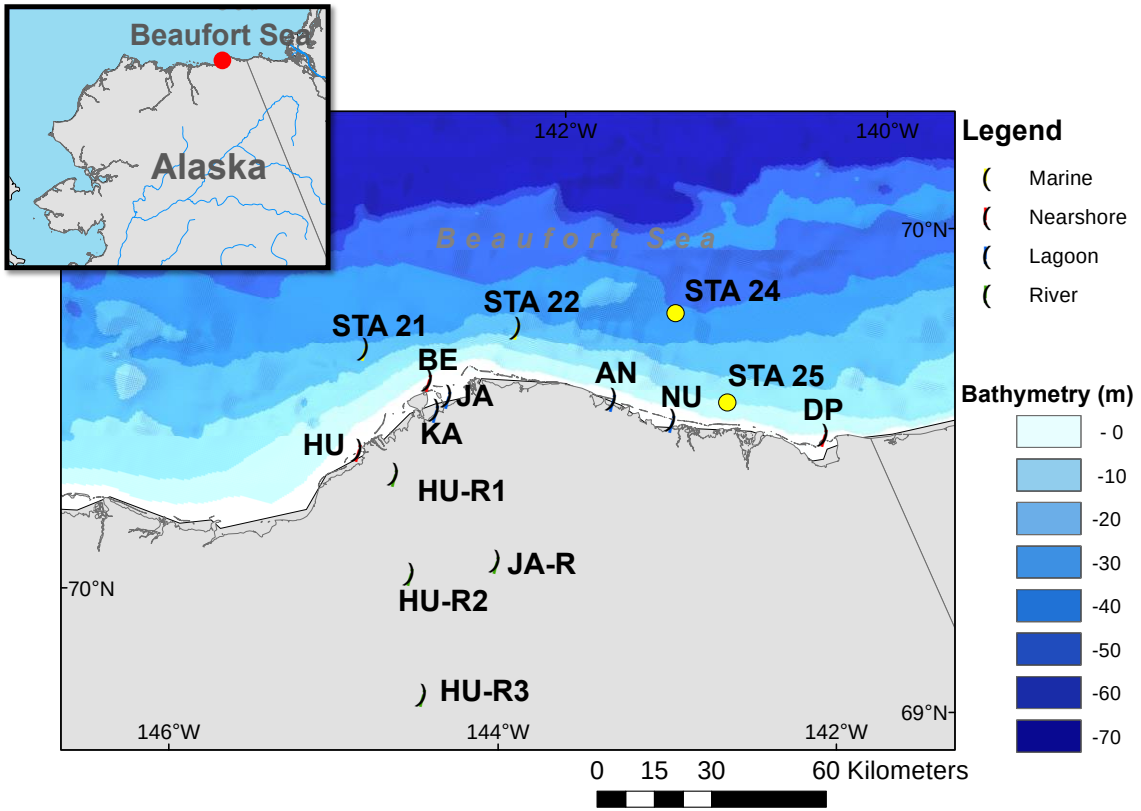

Figure 2.1 Lagoon, nearshore, marine, and river sites along the coast of the eastern Alaskan Beaufort Sea. See Table 2.1 for station code definitions. Organic matter (all sites) and animal samples (nearshore, lagoon and Hulahula River sites only) were collected in August 2011-2014 for C and N isotope analysis.

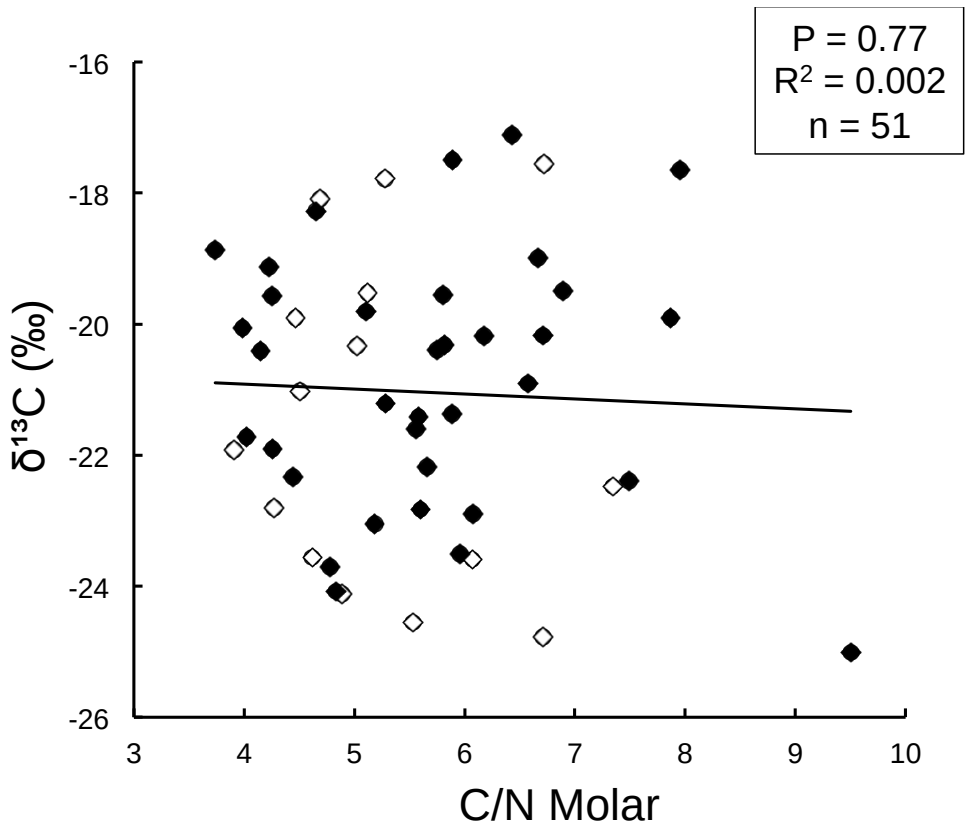

Figure 2.2 Relationship between C:N molar ratio and $\delta^{13}C$ (‰).
Genera collected from lagoon (closed symbols) and nearshore (open symbols) sites are shown (data from Tables 2.4 and 2.5). Linear regression through all data points is not significant.

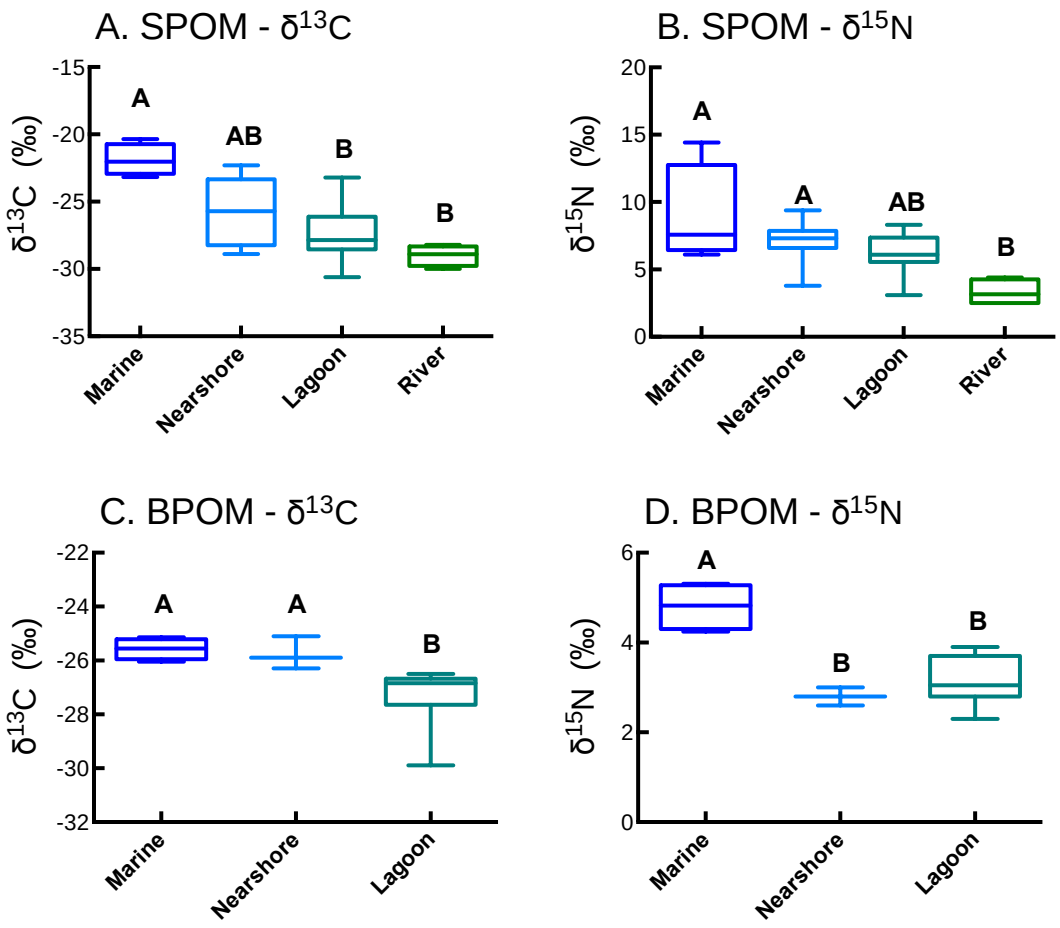

Figure 2.3 C and N stable isotopes boxplots.
Mean (line), lower and upper quartile (box), and minimum, maximum (whiskers) for SPOM and BPOM collected in August are shown. Groups that do not share a letter are statistically different as determined with Kruskal-Wallis analysis with Dunn's multiple comparison post-hoc test.

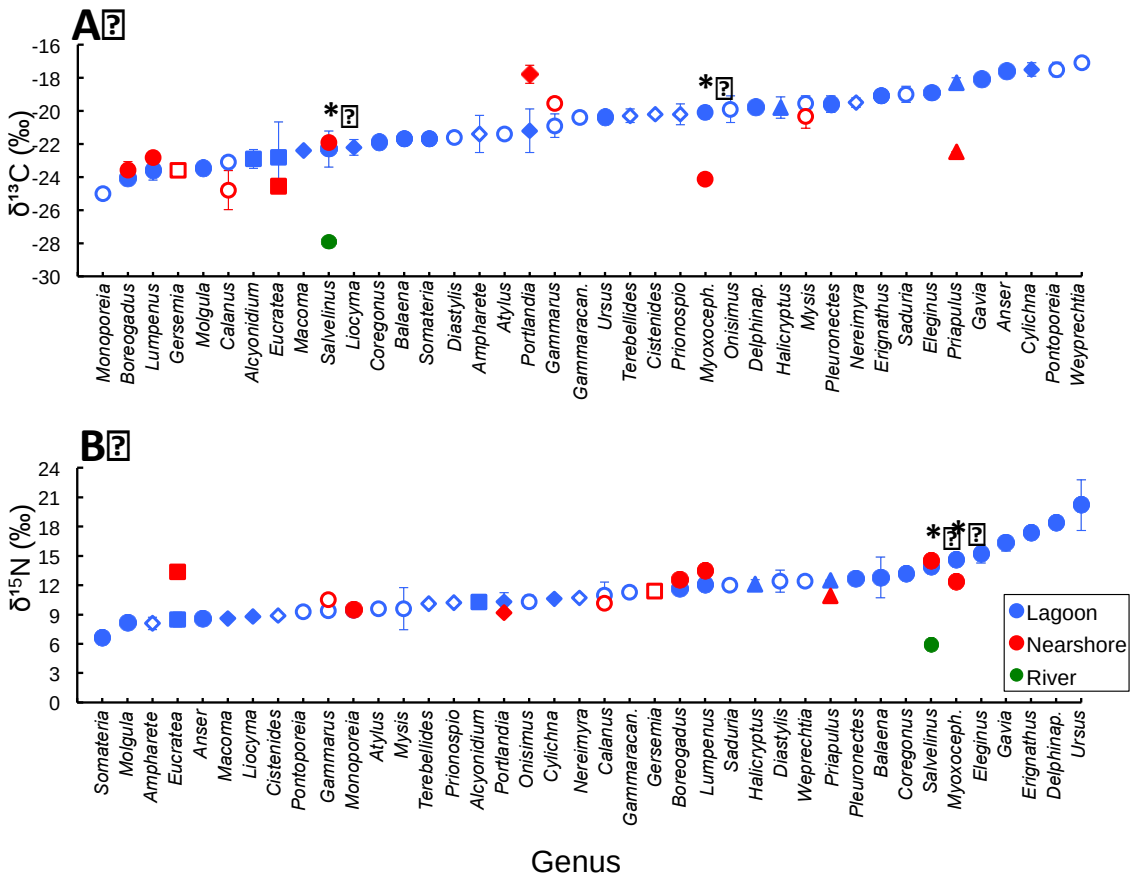

Figure 2.4 Mean (± SE) $\delta^{13}C$ (A) and $\delta^{15}N$ (B) of taxa collected in August from lagoon, nearshore, or river sites.

Symbols denote phyla (Annelida (◇), Arthropoda (O), Bryozoa (■), Cephaloryncha (Δ), Chordata (●), Cnidaria (□), Mollusca (◆). Data compiled from Table 3. * Indicates taxa differed significantly between nearshore and lagoon sites (or between lagoon and river sites in the case of *Salvelinus*).

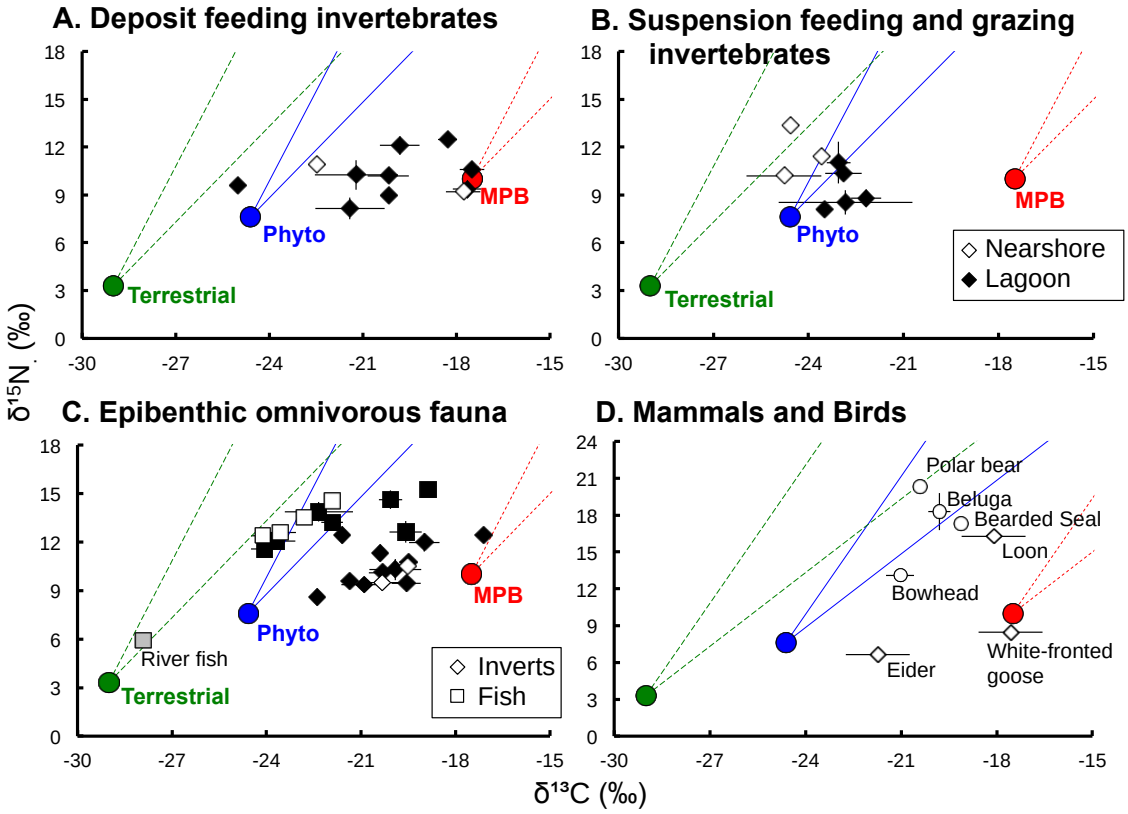

Figure 2.5 Stable isotope biplot for animals and OM sources collected in August (open symbols = nearshore sites, closed symbols = lagoon sites).
A. surface and subsurface deposit feeding invertebrates (De/SS), B. suspension feeders and grazing invertebrates, C. epibenthic omnivorous invertebrates (diamonds) and fishes (squares; river fish are shaded square), and D. birds and marine mammals (note panel D has an expanded y-axis). Each point represents one genus (mean ± SE) within the feeding guild. Basal carbon sources are $C_{Terrestrial}$ (river SPOM), $C_{Phytoplankton}$ (20um net sample), and C_{MPB} (literature values). Enrichment lines originate from each carbon source and show the expected transfer of OM assuming trophic enrichment factors of 0.8 - 2‰ for $\delta^{13}C$ and 3 - 4‰ for $\delta^{15}N$.

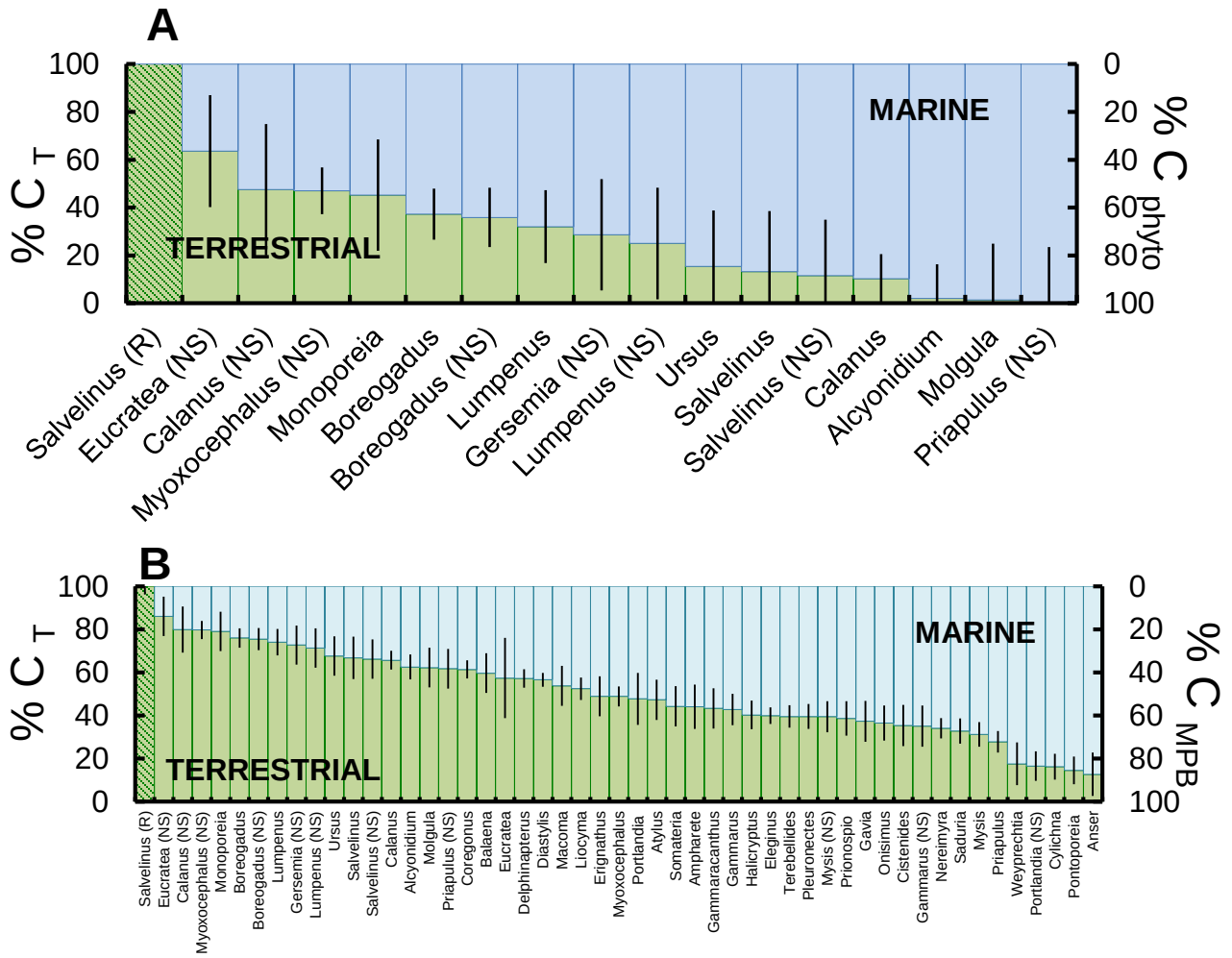

Figure 2.6 Mean (± SE) % C_T and % C_M using $C_{phytoplankton}$ (panel A) or C_{MPB} (panel B) as the marine end-member for taxa collected in August from lagoon, nearshore, and river sites.

Only taxa with % C_T > 1 are shown. These percentages were generated using IsoError—a two endmember mixing model using $\delta^{13}C$ as a source indicator. Nearshore (NS) and river (R) biota are labeled, all others are from lagoon sites.

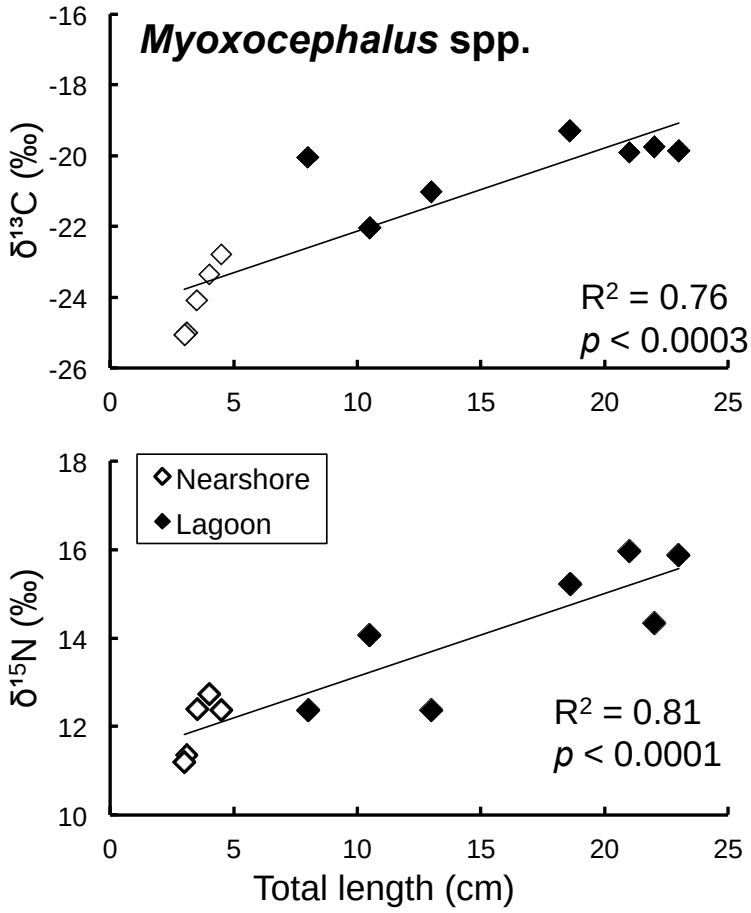

Figure 2.7 Relationship between total length and C and N isotope value for *Myoxocephalus* species collected from lagoon and nearshore sites in August 2011-2014

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